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THE HOSTS, LIFE HISTORY AND CONTROL OF THE CEDAR-APPLE RUST FUNGUS GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE SCHW.

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With two text figures and plates 91-98

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I. INTRODUCTION

Gymnosporangium Juniperi-virginianae Schw. and the diseases caused by it have long been known to mycologists and phytopathologists. *Gymnosporangium Juniperi-virginianae* was first described on *Juniperus virginiana* L. by Schweinitz in 1822 and on *Malus coronaria* Mill. under the name *Caeoma* (*Aecidium*) *pyratum* by the same author in 1832. Experimental demonstration of these as two phases of the same organism was made independently by Halsted and by Thaxter in 1886. Shortly after the results of their experiments were published (1887) eradication of the red cedars adjacent to orchards was recommended as a protection to apples. Their findings have been repeatedly confirmed and the eradication of red cedars as an effective protective measure has been proved and widely practised. It is almost solely from this point of view that *G. Juniperi-virginianae* has been regarded up to the present.

In recent years there have been persistent demands for information on *G. Juniperi-virginianae* with reference to the pathogenicity and control of this organism on various species of *Malus* employed as ornamentals and also on species of *Juniperus*, particularly the eastern red cedar. There has likewise been a recognition of the difficulties and disadvantages attendant on red cedar eradication, and growing out of that a demand for more satisfactory control measures. These desiderata have served as the stimulus that led to the investigations outlined in this paper.

The main lines of my investigations are as follows:

1. A determination by means of cultures of the species of pomaceous hosts susceptible to *G. Juniperi-virginianae*, and for those that are susceptible, their degree and their period of susceptibility.

2. Field observations on the susceptibility of species of *Juniperus* to *G. Juniperi-virginianae*.

3. A study of the geographical range and symptomatology of the diseases caused by *G. Juniperi-virginianae*.

4. A detailed inquiry into the life history of *G. Juniperi-virginianae* and a cultural study of biological strains.

5. Observations on factors influencing the amount of infection on the hosts of *G. Juniperi-virginianae*.

6. The testing of fungicidal control measures.

II. A DETERMINATION BY MEANS OF CULTURES OF THE SPECIES OF POMACEOUS HOSTS SUSCEPTIBLE TO G. JUNIPERI-VIRGINIANAE

Such knowledge as we have of the pomaceous hosts of *G. Juniperi-virginianae* as determined by cultures is due mainly to the work of Halsted, Thaxter, Pammel and Arthur. Halsted (1886) successfully cultured *G. Juniperi-virginianae* on *Malus coronaria* in 1886. Thaxter (1887) made successful cultures on *M. pumila* (*M. Malus*). He also inoculated *Sorbus americana, Aronia arbutifolia* (*Pyrus arbutifolia*), *Crataegus coccinea* and *Amelanchier canadensis* but with negative results. Pammel (1905) stated that he inoculated *G. Juniperi-virginianae* on *M. ioensis, M. ioensis* "Soulard Crab," *M. pumila* (*M. Malus*), *Crataegus mollis, C. pinnatifida, C. punctata, Sorbus Aucuparia, Pyrus communis* and *Amelanchier alnifolia.* He reported infection on *M. ioensis, C. mollis* and *C. pinnatifida,* but the inclusion of the two latter species as hosts of *G. Juniperi-virginianae* is open to question. Bliss (1933) also doubts the validity of these species as hosts. The photographs and descriptions of the fructifications on *C. mollis* and *C. pinnatifida* closely resemble *G. globosum* Farl. *Pyrus melanocarpa* = *Aronia melanocarpa,* has likewise been recorded as a host of *G. Juniperi-virginianae* (Plant Disease Reporter 12:71. 1928). I have examined the collection on which the report is based and find the fungus to be *G. clavipes* C. & P. I am not including these species as hosts of *G. Juniperi-virginianae.* All of the other species listed by Pammel remained free from infection. Arthur (1908, 1909) confirmed the work of Halsted and Thaxter as to *M. coronaria* and *M. pumila* respectively.

It will be seen from the foregoing that *M. coronaria, M. pumila* and possibly *M. ioensis* have already been culturally established as hosts of *G. Juniperi-virginianae.* Other workers have reported additional hosts from observations made in the field. Farlow (1880) reported that *M. angustifolia* was susceptible in Massachusetts. Kern (1911) added *M. baccata* to the list of known hosts. Haskell (1919) reported *M. floribunda* (*Pyrus pulcherrima*) as a host. Adams (1921) found that *M. glaucescens* was susceptible in Pennsylvania. Martin (1926, 1928) reported *M. spectabilis* var., also *M. Sargenti* and *M. arnoldiana* as hosts. Blain (1931) stated that *M. sylvestris* was also susceptible, and Bliss (1933) reported that "pycnidia formed occasionally" on *M. spectabilis* (*Pyrus spectabilis*). In addition to the *Malus* hosts Johnson (1909) reported *Pyrus communis* and Patterson (1922) reported *P. glauca,* but I cannot find a reference to such a species as the latter. The incorporation of *Malus baccata, M. floribunda, M. Sargenti, M.*

arnoldiana, Pyrus communis and *P. glauca* as hosts, however, are not in accordance with my findings. Further than these cultures and field observations, no authentic information is available as to the susceptibility of most of the species of the genus *Malus*. In order to fill this gap, an extensive series of cultures was made on as many species of *Malus* as possible. Fortunately all but two or three of the known species were available for testing in the Arnold Arboretum of Harvard University where this experimentation was exclusively conducted. Because of the fact that species of other genera were reported as hosts to *G. Juniperi-virginianae* (as noted above), the tests were extended to several other pomaceous genera. The complete list comprises 17 species and varieties of *Amelanchier*, 1 of *Crataegomespilus*, 1 of *Cydonia*, 75 of *Malus*, 1 of *Photinia*, 19 of *Pyrus*, 2 of *Sorbaronia* and 17 of *Sorbus*. One species of *Comptonia* and two of *Myrica* were also inoculated. In addition, field notes were made on all species of *Crataegus* (942) growing in the Arnold Arboretum.

The cultures in all instances were conducted on undisturbed trees in the Arnold Arboretum. Small branches were inoculated and the rest of the crown served as controls. In the inoculation work celluloid cylinders as described by Hubert (1916) were used, but in plugging them sphagnum moss was substituted for cotton. They made satisfactory and efficient moist chambers for spore germination on the trees under field conditions. A two ounce vaseline jar proved to be a convenient container for carrying the inoculum. The latter was applied to the plant parts by means of a camel's hair brush.

In preparing the inoculum the galls of *G. Juniperi-virginianae* employed were gathered fresh from red cedar trees or taken from a store in a refrigerator. The teliospores, when kept at approximately 4°C., remained viable for a period up to nine months. From twenty to thirty telia were plucked from the galls and dropped into tap or distilled water in the inoculum bottle. After the telia had become partially softened by gelatinization, a process requiring about five minutes, they were crushed against the side of the bottle with the finger and this provided a uniform suspension of the teliospores. The inoculum was then ready for use. It would remain in good condition for two to three hours after which a fresh lot was prepared. The first inoculations were made soon after the leaves emerged from the buds, and inoculations were repeated periodically on other leaves as long as they remained susceptible to infection.

For inoculating, a branch was selected and tagged and an abundance of inoculum was applied to the leaves, flowers or fruit and stem with the camel's hair brush. The twig was inserted in the inoculation tube

which was then plugged with wet sphagnum and tied to the underside of a nearby branch for support and to protect the enclosed twig from excessive heating by the sun. The tubes were left on the inoculated twigs for two or three days. With this technic positive results were almost certain if the hosts were inoculated while the young parts were still within their period of susceptibility. The heavy sowing of teliospores combined with a very moist atmosphere and cool temperatures gave almost optimum conditions for the germination of the spores.

In recording data the inoculated plants were classified according to five categories or degrees of relative susceptibility. These groups were designated by symbols and defined as follows:

0—immune, no fructifications formed.
s—only abortive spermogonia formed.
1—resistant, from one to five aecia per sorus.
2—moderately susceptible, five to twenty-five aecia per sorus.
3—very susceptible, twenty-five or more aecia per sorus.

A complete enumeration of all species and varieties of inoculated plants, and of four species of *Malus* (marked by *) not inoculated but examined for natural infection, on which the results were negative were as follows:

Amelanchier amabilis Wieg., *A. asiatica* Endl., *A. Bartramiana* Roem., *A. Bartramiana* × *laevis, A. canadensis* Med., *A. florida* Lindl., *A. grandiflora* Rehd., *A. humilis* Wieg., *A. humilis* × *sanguinea, A. intermedia* Spach., *A. laevis* Wieg., *A. oblongifolia* Roem., *A. ovalis* Med., *A. sanguinea* DC., *A. sera* Ashe, *A. spicata* K. Koch, *A. stolonifera* Wieg.

Crataegomespilus grandiflora Bean.

Crataegus (942 species) A complete enumeration will appear in an article by J. D. MacLachlan.

Cydonia oblonga Mill.

Malus arnoldiana Sarg., *M. asiatica* Nakai, *M. atrosanguinea* Schneid., *M. baccata* Borkh., *M. baccata costata* Hort., **M. baccata gracilis* Rehd., *M. baccata Jackii* Rehd., *M. baccata mandshurica* Schneid., **M. baccata microcarpa* Regel, *M. baccata pendula* Hort., *M. brevipes* Rehd., *M. flexilis* Hort., *M. florentina* Schneid., *M. floribunda* Sieb., *M. Halliana* Koehne *Parkmanii* Rehd., *M. Halliana spontanea* Rehd., *M. Hartwigii* Koehne, *M. honanensis* Rehd., *M. hupehensis* Rehd., *M. kansuensis* Schneid., *M.* spec. (*Pyrus Malus laurifolia* Gibbs), *M.* spec. (*Pyrus Lemoinei* Hort.), *M. magdeburgensis* Schoch, *M. micromalus* Mak., *M. orthocarpa* Lavall., *M. Prattii*

Schneid., *M. pumila* Mill., *M. pumila Niedwetzkyana* Schneid., *M. purpurea* Rehd., **M. purpurea aldenhamensis* Rehd., *M. purpurea Eleyi* Rehd., *M. robusta persicifolia* Rehd., *M. Sargenti* Rehd., *M. Scheideckeri* Zabel, *M. Scheideckeri "Excellenz Thiel," M. sikkimensis* Koehne, *M. spectabilis* Borkh., *M. spectabilis Riversii* Nash, *M. sublobata* Rehd., *M. toringoides* Hughes, *M. trilobata* Schneid., *M. Tschonoskii* Schneid., *M. yunnanensis* Schneid., **M. yunnanensis Veitchii* Rehd., *M. zumi* Rehd., *M. zumi calocarpa* Rehd.

Photinia villosa DC.

Pyrus amygdaliformis Vill., *P. Balansae* Decne., *P. betulifolia* Bge., *P. Bretschneideri* Rehd., *P. communis* L., *P. denticulata* Hort. Angl. ex Dum.-Cours., *P. elaeagrifolia* Pall., *P. Korshinskyi* Litv., *P. Lindleyi* Rehd., *P. longipes* Coss. & Dur., *P. Michauxii* Bosc, *P. nivalis* Jacq., *P. pashia* Buch.-Ham., *P. phaeocarpa* Rehd., *P. salvifolia* DC., *P. serotina* Rehd., *P. serrulata* Rehd., *P. syriaca* Boiss., *P. ussuriensis* Maxim.

Sorbaronia alpina Schneid. *superaria, S.* spec.

Sorbopyrus auricularis bulbiformis Schneid.

Sorbus americana Marsh., *S. Aria* Crantz., *S. arnoldiana* Rehd., *S. Aucuparia* L., *S. commixta* Hedl., *S. decurrens* Hedl., *S. discolor* Hedl., *S. dumosa* Greene, *S. hybrida* L., *S. intermedia* Pers., *S. japonica* Koehne *calocarpa* Rehd., *S. Matsumurana* Koehne, *S. Meinichii* Hedl., *S. pohuashanensis* Hedl., *S. rotundifolia* Hedl., *S. subpinnata* Hedl., *S. thuringiaca* Fritsch.

Other plants inoculated were *Comptonia asplenifolia* Ait., *Myrica carolinensis* Mill. and *M. Gale* L.

The results of the successful inoculations as well as examinations of plants in the Arnold Arboretum for natural infections show that the pomaceous hosts of *G. Juniperi-virginianae* were found in the genus *Malus* only (*Malus* as limited by Rehder 1927). These hosts were divided into two groups according to the degree of development of the aecial phase of the rust. These groups were A, those hosts that produced both spermogonia and aecia, and B, those hosts that produced spermogonia only.

A complete list of the pomaceous hosts of *G. Juniperi-virginianae* is presented in table I.

Studies of the hosts in groups A and B, as given in table I, reveal several interesting facts.

(a) A remarkable correlation is found to exist between the hosts in group A and their taxonomic position. Taxonomically, these hosts, with the exception of *M. fusca* and *M. sylvestris,* belong to the section

Chloromeles Rehd. of the genus *Malus;* indeed, they comprise all of the known species and varieties of that section.

(b) Another striking correlation is brought to light when the geographical distribution of the hosts in group A is taken into consideration, namely, it is found that these plants are native to North America only. In fig. 1 is shown an outline map of North America upon which the natural geographical distribution of these hosts has been plotted as vertical lines. It will be seen from this map and its accompanying description that, at the present time, the geographical distribution of *G. Juniperi-virginianae* extends completely over the coinciding ranges of the native species of *Malus* and the eastern red cedar. *Malus fusca,* native to the Pacific coast region of North America, and *M. sylvestris* of Europe, were the only species outside the section Chloromeles on which aecia were consistently produced. It is noteworthy, however, that *M. fusca* and *M. sylvestris* proved to be the most resistant species of group A.

TABLE I.

A COMPLETE LIST OF THE KNOWN POMACEOUS HOSTS OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE SCHW.

Group A, containing those hosts on which both spermogonia and aecia were produced.

	Degree of susceptibility		Degree of susceptibility
Malus		Malus	
angustifolia Michx.	2	ioensis Britt.	2
*arnoldiana Sarg.		**ioensis	
*baccata Borkh.		Palmeri Rehd.	3
bracteata Rehd.	2	ioensis plena Rehd.	3
coronaria Mill.	2	lancifolia Rehd.	2
coronaria		platycarpa Rehd.	2
Charlottae Rehd.	3	platycarpa	
coronaria		Hoopesii Rehd.	2
elongata Rehd.	2	*Sargenti Rehd.	
Dawsoniana Rehd.	1	Soulardi Britt.	3
*floribunda Sieb.		sylvestris Mill.	1
fusca Schneid.	1	Pyrus	
glabrata Rehd.	2	*communis L.	
glaucescens Rehd.	2	*glauca	

Also many orchard varieties of apples.

*These hosts were reported by other workers, but were not observed as susceptible in the Arnold Arboretum.
**Observed from herbarium material in the Arnold Arboretum.
1—resistant, from one to five aecia per sorus.
2—moderately susceptible, from five to twenty-five aecia per sorus.
3—very susceptible, from twenty-five or more aecia per sorus.

Group B, containing those hosts on which spermogonia only were produced.

Malus	Malus
adstringens Zabel	pumila apetala Schneid.
astracanica Dum.-Cours.	pumila pendula
prunifolia Borkh.	"Elise Rathke"
prunifolia	robusta Rehd.
fastigiata Rehd.	Sieboldii Rehd.
prunifolia fructu coccineo	Sieboldii arborescens Rehd.
prunifolia rinki Rehd.	Sieboldii × spectabilis
*pumila Mill.	*spectabilis Borkh.

(c) Equally striking correlations are found to exist between the hosts in group B and their taxonomic position and geographical distribution. In table II are presented certain data on the hosts on which spermogonia only were produced. An examination of column two of this table will show that taxonomically all of these hosts are restricted to the sections Eumalus Zabel and Sorbomalus Zabel of the genus *Malus*. Geographically, none of these hosts are native to North America; all are confined to Eurasia.

(d) The phenomenon of genetic inheritance of susceptibility to the aecial phase of *G. Juniperi-virginianae* seems to be common to hosts in both groups. In the Malus collection in the Arnold Arboretum only two species that developed aecia (therefore placed in group A) originated by hybridization. These species are *M. Dawsoniana* (*M. fusca* × *pumila*) and *M. Soulardi* (*M. ioensis* × *pumila*). Of the parents of *M. Dawsoniana, M. fusca* was very resistant but produced both spermogonia and aecia (table III), while *M. pumila* produced spermogonia only (table I). *Malus Dawsoniana* was very resistant but developed aecia as did its more susceptible parent and in an even shorter period of time (table VII). Of the parents of *M. Soulardi, M. ioensis* was moderately susceptible and produced both spermogonia and aecia (table II), while *M. pumila* produced spermogonia only (table I). *Malus Soulardi* proved to be very susceptible and also produced aecia in a shorter time than its more susceptible parent.

Turning now to the parentage of some of the hybrid species listed in group B (those on which spermogonia only were produced), interesting data are recorded in column three of table II. It is noteworthy that when *M. pumila* and *M. Sieboldii* are crossed with the immune species *M. baccata* and *M. spectabilis* respectively, the hybrid offsprings react towards *G. Juniperi-virginianae* as do the susceptible parents. Here, just as in the cases of hybridization cited for group A, susceptibility to infection by *G. Juniperi-virginianae* seems to be a dominant character. Other crosses between species that produced spermogonia only and immune species as, for example, *M. atrosan-*

guinea (*M. Halliana* × *Sieboldii*) and *M. zumi* (*M. baccata mandshurica* × *Sieboldii*) have resulted in hybrids that so far have proved to be immune. All of the data bearing on this phenomenon, however, indicate that susceptibility to *G. Juniperi-virginianae* was probably due to a complex genetic constitution. (See Crane and Lawrence, 1933.)

(f) A footnote to table II states that *M. prunifolia fastigiata* produced a few abortive aecia. Although this variety was inoculated fourteen times on six different dates, only a single inoculation resulted in the production of aecia. In my judgment, however, this variety should be included with group B because the production of aecia could not be experimentally repeated.

TABLE II.

PRESENTING DATA ON THE HOSTS OF G. JUNIPERI-VIRGINIANAE IN THE GENUS MALUS WHICH PRODUCED SPERMOGONIA ONLY

Host	Taxonomic position	Parentage	Time for development of the spermogonia		Geographical distribution
			Appeared	Oozing	
adstringens	Eumalus	baccata x pumila	30*	--	
astracanica	"	pumila x prunifolia	46	--	
prunifolia	"	a species	16-34	46	eastern Asia
prunifolia fastigiata	"	var. of prunifolia	15-44	20-30**	"
prunifolia fructu coccineo	"	var. of prunifolia	18-22	28-33	"
prunifolia rinki	"	var. of prunifolia	22-33	--	"
pumila apetala	"	var. of pumila	15-37	29	Eurasia
pumila pendula "Elise Rathke"	"	var. of pumila	35	--	"
robusta	"	prunifolia x baccata	61	--	"
Sieboldii	Sorbomalus	a species	26-33	--	Japan
Sieboldii arborescens	"	var. of Sieboldii	19-30	--	Japan and Korea
	"	Sieboldii x spectabilis	21-29	--	

*Figures refer to the number of days after inoculating.
**A few aecia appeared in 62 to 68 days.

III. PRELIMINARY INVESTIGATIONS ON THE DURATION OF A PERIOD OF SUSCEPTIBILITY IN APPLE LEAVES.

Fulton (1913), Reed and Crabill (1915) and Giddings and Berg (1915) have reported that leaves of orchard apples are susceptible to infection by *G. Juniperi-virginianae* for only a brief period in their youth. For the purpose of further investigations, five series of inoculations were made with *G. Juniperi-virginianae* on certain species and

TABLE III.

PRELIMINARY DATA ON "PERIOD OF SUSCEPTIBILITY"

	Approximate dates of inoculating										
Host	May 1		May 19		June 11		July 11		Aug. 2		deg. susc.
	spm	aec	spm	aec	spm	aec	spm	aec	spm	aec	
MALUS											
ioensis plena	*	*	*	*	*	*	*	*	*	*	3
coronaria Charlottae	*	*	*	*	*	*	*	*	*	*	3
angustifolia			*	*	*	*	*	*	*	0	3
glaucescens	*	*	*	*	*	*	*	*	0	0	2
glabrata	tags lost		*	*	*	*	*	*	-	-	2
ioensis coronaria elongata	*	*	*	*	*	*	*	0	0	0	2
coronaria	*	*	*	*	*	*	*	0	-	-	2
Soulardi	*	*	*	*	*	*	0	0	0	0	2
platycarpa			*	*	*	0	-	-	-	-	2
sylvestris	*	*	*	*	*	0	-	-	-	-	1
fusca	*	*	*	0	*	0	-	-	-	-	1
prolific	*	*	*	0	0	0	-	-	-	-	1
Sieboldii x spectabilis	-	-	*	0	*	0	-	-	-	-	s
Sieboldii arborescens	*	0	*	0	*	0	-	-	-	-	s
prunifolia fastigiata	*	*	*	0	*	0	0	0	-	-	s
Sieboldii			*	0	0	0	-	-	-	-	s
pumila pendula	0	0	*	0	0	0	-	-	-	-	s
pumila apetala		0	*	0	0	0	-	-	-	-	s
prunifolia fructu coccineo	*	0	*	0	0	0	-	-	-	-	s
prunifolia	*	0	*	0	0	0	-	-	-	-	s
robusta	*	0	0	0	0	0	-	-	-	-	s
prunifolia rinki	*	0	0	0	0	0	-	-	-	-	s
astracanica	*	0	0	0	0	0	-	-	-	-	s
adstringens	*	0	0	0	0	0	-	-	-	-	s
Totals *	19	11	21	11	15	9	8	6	3-5	2-4	
0	1	9	4	14	10	16	17	19	22-20	23-21	
Grand totals	* 30		32		24		14		5-7		
	0 10		18		26		36		45-43		
Percentage successful inoculations	75%		64%		48%		28%		10%-14%		

*, successful cultures; 0, negative results; -, not inoculated.

varieties of hosts in the Arnold Arboretum. Inoculations were made in the manner previously described, the inoculum being kept in a refrigerator during the summer.

It may be argued that the viability of the teliospores decreased during this period and thereby may have had influence upon infection of the leaves. This influence was probably slight, however, since the younger leaves of the very susceptible varieties *M. coronaria Charlottae* and *M. ioensis plena,* seemed to be almost as susceptible in August as in May.

The data on these inoculations are presented in full in table III. That a period of susceptibility existed in the early stages of growth of the leaves is demonstrated by the fact that the greater number of successful inoculations resulted early in the growing season. The total number of positive inoculations as compared with the negative inoculations were in the approximate percentages of 75%, 64%, 28% and 10% to 14% for the inoculations made on May 1, May 19, June 11, July 11 and August 2 respectively. The last percentage is given in pair because certain of the plants that proved to be susceptible in July were not inoculated in August.

The duration of the period of susceptibility varied for the different species and varieties of *Malus*. The more resistant ones were susceptible until about June 1; the moderately susceptible species and varieties were susceptible until about July 1; and the most susceptible could be infected throughout the greater part of the growing season.

IV. OBSERVATIONS ON SPECIES OF JUNIPERUS SUSCEPTIBLE TO G. JUNIPERI-VIRGINIANAE

Our knowledge of the *Juniperus* hosts of *G. Juniperi-virginianae* as determined by cultural studies is due solely to the work of Dodge (1918) and Bliss (1933). These investigators successfully cultured *G. Juniperi-virginianae* on *J. virginiana* L. Heald (1909) and Weimer (1917) also inoculated red cedars but with no positive results. Several other workers, however, reported additional hosts as a result of field observations. Stone (1909) reported *J. bermudiana* (*J. barbadensis*). Kauffman (1916) stated that *J. communis* was susceptible. The recognition of these species as hosts, however, is open to question. Reed and Crabill (1915) reported *J. virginiana Schottii, J. virginiana glauca* and *J. virginiana fastigiata* from Virginia. Hahn, Hartley and Pierce (1917) found that specimens of *J. scopulorum* (the western red cedar) introduced into Illinois became infected. Arthur

(1926) and Bliss (1933) also found that introduced plants of *J. scopulorum* were susceptible to *G. Juniperi-virginianae*. Bliss further reported *J. virginiana elegantissima, J. virginiana globosa, J. virginiana Canaertii* and *J. virginiana Hillii* as susceptible in Iowa. He also examined other varieties of *J. virginiana* as well as species and varieties of *J. communis, J. excelsa, J. chinensis* and *J. horizontalis* and several unidentified species but found them to be immune. Further than the foregoing cultures and field observations, no authentic information is available as to the susceptibility of other species and varieties of *Juniperus*.

In order to add to the information just cited, field observations were made on the extensive *Juniperus* collections at the Arnold Arboretum. In 1933 each individual cedar was examined for infection and the species and varieties were recorded in immune and susceptible groups. The immune species and varieties of *Juniperus* are as follows:

Juniperus chinensis L., *J. chinensis globosa* Hornibrook, *J. chinensis japonica* Lav., *J. chinensis mas* Gord., *J. chinensis pendula* Franch., *J. chinensis Pfitzeriana* Spaeth., *J. chinensis plumosa* Hornibrook, *J. chinensis plumosa aurea* Hornibrook, *J. chinensis pyramidalis* Beiss., *J. chinensis Sargenti* Rehd., *J. chinensis Watereri* Hort., *J. communis* L., *J. communis Ashfordii* Hort., *J. communis aurea* Nichols., *J. communis aureo-spica* Rehd., *J. communis compressa* Carr., *J. communis cracovica* Hort., *J. communis depressa* Pursh, *J. communis hibernica* Gord., *J. communis montana* Ait., *J. communis oblongo-pendula* Sudw., *J. communis oblonga* Loud., *J. communis pyramidalis* Hort., *J. communis suecica* Ait., *J. conferta* Parl., *J. formosana* Hayata, *J. horizontalis alpina* Rehd., *J. horizontalis glomerata* Rehd., *J. horizontalis variegata* Hort., *J. procumbens* Sieb., *J. rigida* Sieb. & Zucc., *J. Sabina* L., *J. Sabina cupressifolia* Ait., *J. Sabina pyramidalis* Hort., *J. Sabina tamariscifolia* Ait., *J. Sabina variegata* Carr., *J. scopulorum horizontalis* D. Hill, *J. squamata* Buch.-Ham., *J. squamata Fargesii* Rehd. & Wils., *J. squamata Meyeri* Rehd., *J. squamata Wilsonii* Rehd., *J. virginiana aurea, J. virginiana Burkii, J. virginiana Canaertii* Sénécl., *J. virginiana Kosteri* Beiss., *J. virginiana pyramidalis glauca, J. virginiana plumosa* Rehd., *J. virginiana tripartita* R. Smith and *J. virginiana venusta* Rehd.

In table IV are given those species and varieties of *Juniperus* susceptible to *G. Juniperi-virginianae*. Those hosts that were not observed as susceptible in the Arnold Arboretum collections, but were reported by other workers, are marked with a star.

TABLE IV.

A COMPLETE LIST OF THE KNOWN JUNIPERUS HOSTS OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE SCHW.

Juniperus	Juniperus
*bermudiana L.	virginiana L.
*communis L.	elegantissima Hochst.
horizontalis Moench.	fastigiata Hort.
Douglasii Rehd.	filifera D. Hill.
plumosa Rehd.	glauca Carr.
scopulorum Sarg.	globosa Beiss.
viridifolia	*Hillii Hort.
var.	pendula Carr.
virginiana L.	polymorpha Hort.
*Canaertii Sénécl.	pyramidalis Carr.
Chamberlaynii Carr.	reptans Beiss.
cinerascens Hort.	Schottii Gord.

*These hosts were reported by other workers, but were not observed as susceptible in the Arnold Arboretum.

In the genus *Gymnosporangium* it is usual to find that all of the telial hosts of any one species are confined to but one section of the genus *Juniperus*. *Gymnosporangium Juniperi-virginianae* follows this general rule, for its hosts (with the exception of the doubtful host *J. communis*) belong exclusively to the section Sabina.

Geographically these hosts, with the exception of *J. communis*, occur only in North America. *Juniperus bermudiana* is found along the Gulf coast of the United States and in Bermuda. *Juniperus virginiana* occurs in eastern North America over the entire geographical range of the pomaceous hosts in the section Chloromeles. *Juniperus horizontalis* occurs over this same territory and even farther north into Canada. *Juniperus scopulorum* is found in western North America west of the great plains region. The geographical distribution of the Juniperus hosts is shown as horizontal lines on the map in fig. 1 (page 188).

V. SYMPTOMATOLOGY AND RANGE OF THE DISEASES CAUSED BY G. JUNIPERI-VIRGINIANAE

1. Morphological Symptomatology—(a) on Pomaceous Hosts.

Both Schweinitz (1832) and Farlow (1880) gave brief descriptions of the gross morphological symptomatology of the disease produced on the leaves of apples. These descriptions seem to have been primarily to aid in the identification of the fungus. Seymour (1886) emphasized the aecial phase of this rust as disease-producing. He described numerous instances in which orchards in the vicinity of red

cedars were severely injured by the rust. Stewart and Carver (1886) also reported serious damage to apple trees and noted further that certain varieties were more susceptible to the rust than others. Thaxter (1887) observed that not only the leaves but also the fruits and twigs were attacked. Pammel (1905) reported a sudden outbreak of the disease in Iowa in 1905. Heald (1909) drew attention to differences in the susceptibility of certain varieties of apple trees and reported that indirect losses as well as direct losses were often very great. Heald also gave a careful description of the symptoms of disease. He found that the rust first showed as yellow spots on the upper surface of the leaves in from seven to ten days after infection and that the spermogonia appeared in a few weeks. With further development the leaf tissues beneath these spots swelled to a cushion one-fourth to one-half inch in diameter and it was on these that the aecia were produced. Heald noted further that on the resistant varieties of apple "the rust spots remain minute and undeveloped for the entire season," also "in certain cases—the leaf tissue is killed at the point of infection."

In the decade from 1910 to 1920, the cedar-apple rust disease was unusually severe on apples in eastern North America. This furnished a great stimulus for further studies as well as ample opportunity for observations on many details of the disease. Several important findings resulted. Fulton (1913) observed that the leaves of many varieties of apples were not susceptible immediately after breaking bud, but in a few days thereafter they entered a brief period of susceptibility; after that they became immune. Reed and Crabill (1915) substantiated Fulton's observations. They also advanced theories of much interest on the nature of the resistance of apple leaves to *G. Juniperi-virginianae*. They expressed the opinion that two types of resistance were present, namely, (a) "some mechanical, morphological or chemical preventative of infection exists in the epidermis while the palisade and mesophyll tissues are a congenial medium for the growth of the parasite." (b) "In the second type infection takes place as in the susceptible varieties, the lesions develop until they are about 1 mm. in diameter and then they cease to enlarge. No mature spermogonia or aecia are produced."

Giddings and Berg (1915) showed that the leaves of certain varieties of apples were immune for the first ten days after unfolding. They add, however, that mature leaves may become infected following insect injuries, needle punctures or on the torn edges of the leaves. They believe that resistance is "due evidently to a thickening and

hardening of the epidermal cells, as well as to other chemical changes in the interior of the leaf." Giddings (1918), after a very extended study, determined that leaves of "York Imperial," variety of orchard apple, were susceptible to rust infection for fifteen to twenty-five days after they unroll from the bud.

Many workers have reported on the relative susceptibility to orchard apples to the cedar-apple rust disease. Among these are Chester (1896), Lloyd and Ridgway (1911), Jones and Bartholomew (1912), Reed and Crabill (1915), Giddings and Berg (1915), Gardner (1925), Thomas and Mills (1929), Miller (1931), Bliss (1933) and many others. These reports, together with those received in letters to the writer from thirty-six state experiment stations, have been compiled as a part of this study and will be presented as a separate publication.

Only one publication, namely, that of Reed and Crabill (1915), deals with the histological symptomatology of cedar-apple rust. Among their most important findings are (a) "the mycelium of the rust fungus in the apple leaf, is much like that in the cedar apple. It is about the same diameter and ramifies through the leaf in the vicinity of the infection, occupying the intercellular spaces and sending haustoria into the cells of its hosts." (b) "The first symptoms of disease appear about one month after infection as small yellow spots on the dorsal surface of the apple foliage. Spermogonia are formed immediately under the upper epidermis of the leaf." (c) "The hypertrophy of the apple leaf is due almost entirely to an excessive enlargement and multiplication of the spongy parenchyma cells. The thickened spots on the leaves begin to be distinct about the first of July and by the middle of that month aecidia which are borne on the ventral surface begin to break open." (d) "The tissues of the apple fruit are also much hypertrophied. Deep down in this layer the aecidia begin to form and after reaching maturity the aecidium is finally pushed bodily out of the fruit leaving a hole in the skin."

From the accounts found in textbooks and in original papers just reviewed it is apparent that the symptomatology of cedar-apple rust on pomaceous hosts is almost exclusively based on phenomena as observed on orchard apples. To these accounts I have little to add. My own studies, however, embracing observations on a wide range of species of *Malus*, have brought additional phenomena to light; hence for the purpose of calling attention to certain variations, comparisons and correlations an extended description of the symptomatology of this disease is presented with all susceptible species of *Malus* studied by me kept in mind.

In the following account of my own work the more nearly average symptomatology as found on the native species and varieties of *Malus* will be described and variations from this will be dealt with in turn.

The first manifestations of the disease were found from six to ten days after inoculation as pale yellow discolorations on the upper surface (rarely on the lower surface) of the young leaves. These discolored spots increased in size and in intensity of color until about the tenth to the fifteenth day after inoculation when the spots, from five to ten mm. in diameter, became dotted with a few to several minute, deep-yellow points. These were the immature spermogonia forming beneath the epidermis. In from three to five more days the spermogonia ruptured the epidermis, and a clear-yellow, sweetish fluid exuded from their tiny ostioles. Throughout the development of the spermogonia the infection spots on the upper surface of the leaf continued to increase in size to a maximum diameter of about fifteen mm. at which time they were usually bordered by a deep-yellow to bright-red peripheral zone. After the spermogonia ceased oozing they usually turned black and appeared not unlike pycnidia of certain ascomycetous fungi.

Following the maturation of the spermogonia, further symptoms of the disease and signs of the fungus were found on the under-surface of the leaf. Immediately beneath the spermogonia the cells of the infected tissue began to increase in size and number. This was manifested as an irregular, more or less hemispherical swelling from two to ten mm. in diameter. This swelling was first observed from twenty-five to thirty-five days after the inoculations were made. The first evidence of the aecia was observed from sixty to seventy days after inoculating as minute swelling of the epidermis on the swollen cushions. Within the next two to four days, the aecia pierced the epidermis and appeared as grayish acuminate cylinders about one mm. in diameter. The peridium of the aecium split along the sides and curved outward, releasing the enclosed brownish aeciospores.

The development of the disease and of the fungus seemed to be correlated directly with the degree and duration of susceptibility of the pomaceous hosts. In the most resistant hosts including the foreign species and varieties of *Malus* and about twenty-seven per cent of the varieties of orchard apples, the lesions developed only to the formation of small, pale-yellowish discolorations, and the fungus to the production of one or but a few abortive spermogonia. In certain of the hosts a few aecia were also produced. These symptoms and signs appeared from a week to a month later than the normal ones. In the fourth column of table II is recorded the time required for the production of

spermogonia on the exotic species and varieties of *Malus* susceptible to *G. Juniperi-virginianae*. In table VII is given the time in days required for the production of aecia on the most resistant as well as other species of *Malus*. In the more susceptible hosts, including most of our native species and about twenty-one percent (as compiled from the literature) of the varieties of orchard apples, the disease developed more rapidly and to a greater extent than average. The symptoms appeared a few days earlier, and even in a shorter time developed to a greater extent and produced more fruiting structures than the more resistant hosts.

To demonstrate these variations mathematically, a very susceptible, a moderately susceptible and a very resistant host were chosen and several pertinent measurements were made of the diseased tissues and of the fungus. These data are presented in table V.

TABLE V.

PRESENTING DATA ON CERTAIN POMACEOUS HOSTS IN THREE CATEGORIES OF SUSCEPTIBILITY

Host	Plate 93	Degree of susceptibility	No. of cushions per Leaf	No. of Aecia per Cushion	No. of Aecia per Leaf	Av. size of cushions in mm.	Size of Aeciospores
Malus	fig.						
coronaria Charlottae	1	3	5.2	76.0	375.2	55.9 x 45.3	26.23μ x 22.37μ
platycarpa	2	2	9.1	11.7	106.5	33.8 x 26.0	24.88μ x 22.08μ
fusca	3	1	1.7	3.6	6.1	usually lacking	24.42μ x 21.25μ

An analysis of these data shows that the amount of infection, the number of fructifications and the size of the aeciospores vary directly with the degree of susceptibility of the hosts.

In plate 93 are shown photographs on diseased leaves of each of the foregoing and other hosts. In table II are presented data derived from inoculations made periodically on species and varieties of *Malus* of all degrees of susceptibility. From this table it is seen that the degree of susceptibility of the host is directly correlated with its period of susceptibility. The most susceptible apples became infected throughout the greater part of the growing season, while the less susceptible ones could be infected over only decreasing periods of time.

With the increase in age, the leaves of all the hosts became more and more resistant. When inoculations were made in mid-summer, many of the very resistant hosts were then found to be immune, while the more susceptible ones reacted to infection as did the less susceptible hosts earlier in the season. Toward the end of the growing season, many of the infections on the leaves of the more resistant hosts died. On September 6, 1932, and about the same date in 1933, many of these dead areas were found on the resistant species *M. fusca, M. sylvestris* and *M. Dawsoniana;* but practically none were found on the susceptible hosts *M. ioensis plena, M. coronaria Charlottae* and *M. angustifolia*. These phenomena indicate that resistance is due, in part at least, to histological changes in the host protoplasm. It should be added, however, that I could detect no significant morphological differences in the leaves of any of the species at any time of the year.

In table VI are listed the species and varieties of apples whose fruits, twigs and buds are attacked. It will be seen that fruit and twig attack are quite common among the native species and varieties of *Malus* as well as among the orchard apples. The forced growth of infected buds is, so far as known to me, found only on hosts of the genus *Malus* other than orchard apples.

While the symptomatology on the apple leaves has been correlated with certain features, that on the fruits, twigs and buds has not, in my experience, been found to be so correlated.

The symptomatology of the disease in the fruits, twigs and forced grown buds now calls for description. The yellow discoloration and spermogonia appeared on the surfaces of the young fruits and pedicels at about the same time as on the leaves of the apples. The infected fruits increased in size and were variously distorted. The hypertrophy, however, soon reached a maximum, and subsequent growth of diseased fruits was greatly lessened. About the time that aecia appeared on the leaf they also matured on the infected fruits. On the fruits, however, they broke through the epidermis among the spermogonia. The lesions were found on any part of the fruit but seemed to be more abundant on the calyx end.

The development of the spermogonia and aecia and the production of the hypertrophied areas were essentially the same on the twigs of the current season as on the fruits. It frequently happened, however, that when a twig was attacked by this rust the infection spread along the twig and involved a lateral or a terminal bud of the coming season. Inoculation experiments showed also that in certain of the most susceptible native apples the unfolding buds of the current season were also

TABLE VI.

SPECIES AND VARIETIES OF APPLE SUBJECT TO FRUIT ATTACK, TWIG ATTACK AND THE FORCED GROWTH OF BUDS CAUSED BY GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE SCHW.

Fruit Attack	Twig Attack	Forced Growth of Buds
MALUS	MALUS	MALUS
angustifolia	angustifolia	angustifolia
bracteata	bracteata	bracteata
coronaria	coronaria	coronaria
Dawsoniana	glabrata	glabrata
glabrata	glaucescens	ioensis
glaucescens	ioensis	ioensis plena
ioensis	ioensis plena	Soulardi
ioensis plena	lancifolia	
lancifolia	Soulardi	
Soulardi		
Orchard Varieties	Orchard Varieties	
Ben Davis	Ada Red	
Delicious	*Arkansas	
Early Harvest	Bayfield	
Esopus	*Benoni	
Gideon	Duchess	
Grimes	Golden Delicious	
Jonathan	*Jonathan	
Oldenburg	*Malinda	
Red Delicious	Missouri Pippin	
Red June	*Okabena	
Rome	*Peerless	
Sutton	*Red Astrachan	
Twenty Ounce	Red June	
Wealthy	Rome	
Winesap	Salome	
Winter Banana	Smith Cider	
Yellow Bellflower	*Stayman	
Yellow Transparent	*Twenty Ounce	
York	*Wagener	
	Wealthy	
	*Whitney	
	*Winter Banana	
	Yellow Bellflower	

*Bliss (1933) reports that only spermogonia were produced on these varieties.

directly infected. When buds became infected they acted in a most peculiar manner, which, so far as I am able to learn, has not been described before. Bliss (1933), however, observed infected buds on *M. ioensis plena* in Iowa. The infected buds swelled greatly, their scales opened and the young parts began to grow. With later development the infected twig increased greatly in diameter but elongated very slightly, the leaves expanded to an irregular shape and were considerably, yet uniformly, thickened; they were pale green in color and very tenacious of their tomentum. The first spermogonia to appear were at the base of the pedicels. In a short time others developed progressively along the petioles, then on the bases of the leaves; finally, they extended over the entire blade. This wave of development and maturity of the spermogonia was followed by a similar wave of development and maturity of the aecia. At certain times one may find all stages of development of both fructifications on the same leaf. The phenomenon of the forced growth of buds seems to be confined to the most susceptible native apples. Of these, *M. ioensis plena* and *M. Soulardi* were particularly susceptible. A count of such infection on a tree of *M. ioensis plena* showed that about fifteen percent of the buds were attacked. A large nursery was visited in which small specimens of *M. ioensis plena* were planted near infected red cedars. Every twig of the apples was found to be attacked and whole rows of the plants were killed outright. I know of no report of the forced growth of buds in orchard varieties of apples. In plate 95 are shown several photographs of forced growth of buds in various stages of development.

These studies on apple other than orchard apples emphasize three important points:

(a) Hosts on which the lesions are of larger than average size are more susceptible than those on which they are characteristically smaller.

(b) Hosts on which the development of the rust is more rapid are more susceptible than those on which it is slower.

(c) The duration of susceptibility is longer on the more susceptible hosts; indeed, duration of susceptibility is to some degree an index of relative susceptibility.

These phenomena likewise exist in orchard apples. It follows then that the more resistant orchard apples require protection during the early part only of the growing season, while the more susceptible varieties should be protected throughout the entire period of spore discharge from the red cedars.

1. Morphological Symptomatology—(b) on Red Cedars.

The symptoms and signs of cedar-apple rust on red cedars were carefully described by Farlow (1880). He was of the opinion that the galls caused by *G. Juniperi-virginianae* on red cedars were modified leaves. The galls "begin to appear about the end of August and often reach a considerable size before winter." He observed great differences in the size of the galls, "some quite small, so that not more than two or three columns can find attachment, but generally the knots grow from half an inch to an inch and a half in diameter before the gelatinous masses break through the surfaces." He continued—"The latter arise a short distance below the surface, and the outer portion of the knot consisting of several layers of cork cells is raised in flattened papillae. By growth of the gelatinous masses, the center of each papilla is ruptured and the columns arise vertically. In by far the majority of cases, the knots gradually dry and drop off after having borne one crop of spores. In rare instances, however, a new knot may grow from one side of the old knot and bear a second crop of spores." Both Farlow and Schweinitz were of the opinion that the galls were annual. Heald (1909), however, showed that they were biennial, requiring approximately twenty-three months between the time of inoculation and the production of spores. Dodge (1918) confirmed Heald's findings in this respect. Reed and Crabill (1915) reported that in rare cases galls have been found to produce a second crop of spores. Bliss (1933), however, reported that he observed that 20% of the smaller galls produce a second crop of telia and added that some galls produced even a third crop.

The problem of immunity and resistance of red cedars to attack by *G. Juniperi-virginianae* has been a matter of considerable speculation. Giddings and Berg (1918) gave an account of certain observations made by Professor H. H. Whetzel with regard to this phenomenon on red cedars. "I observed that certain cedar trees were badly infected, being loaded with galls, large and small, on all their twigs and branches. A few years later, to my astonishment they were practically free from galls, while others nearby that had borne no galls before were now badly covered with them. What the explanation of this phenomenon is I do not know." Reed and Crabill (1915) stated, "The great difference in susceptibility of cedar trees seems to be individual. Susceptibility also seems to be cumulative. A tree once infected becomes increasingly susceptible from year to year as the increasing number of cedar apples indicate." On the other hand Giddings and Berg (1915) wrote "In sections where the rust is destructive, it is quite common

to see cedar trees with few or no galls, while other trees within a few feet are actually loaded down with them. Close observation of these 'immune' cedar trees has led up to believe that such immunity as they possess is often a direct result of previous heavy infections." They also state "if the tree has been severely diseased with this rust for two or more successive seasons, its growth is greatly inhibited and the opportunity for infection would be proportionately reduced."

The histological structure of the cedar-apple galls caused by *G. Juniperi-virginianae* has attracted much attention. Farlow (1880), Sanford (1888), Coons (1912), Reed and Crabill (1915), Giddings and Berg (1915) and Weimer (1917) are of the opinion that cedar-apple galls are modified leaves. Wörnle (1894) and Heald (1909) believe that the galls originated in the stem of cedar trees; while Stewart (1915) concludes that the galls are modified axillary buds.

To the symptomatology of the disease as recorded in the literature, referred to above, I now add certain field observations of my own.

On red cedars the symptoms and signs are restricted to the needles and adjacent twig tissues of the host plant. The earliest morphological symptoms of disease were observed about the middle of June in Massachusetts. These appeared as slightly swollen green lesions on the adaxial surfaces of the leaves. On the scale-like leaves these swellings were very difficult to detect, and as they increased in size it appeared as if the galls were primarily twig infections. On the subulate leaves, however, it was evident that the lesions or galls were primarily foliar in origin. During subsequent growth the galls increased rapidly in size always retaining a more or less globose form, though they were often considerably infolded or convoluted. The color of the galls gradually changed from a light dull-green of the early summer to a dull, chocolate brown of the fall and winter. The features of a change of color from greenish to brown and a constantly dull surface served to distinguish the gall caused by *G. Juniperi-virginianae* from another gall form in this region, namely, the gall caused by *G. globosum* Farl. The latter retains a deep-brown varnished surface during the entire first season of growth.

Towards the end of the growing season, the galls caused by *G. Juniperi-virginianae* formed characteristic, shallow, circular depressions on their surfaces and in the center of each depression a low papilla developed. These phenomena were typical of the larger galls in winter condition. Many of the smaller ones, however, did not form these depressions until the early spring and some seemed never to have formed them at all. During early March the papillae increased in

diameter and height and became very conspicuous. In the first warm rains of late March and early April the swollen papillae were ruptured, usually by a single slit, and the underlying brownish sorus was exposed to view. During subsequent rains the telia progressively protruded and expanded as yellow gelatinous masses to a maximum of three to five mm. in diameter by about thirty to fifty mm. in length. Upon drying, the telia contracted to distorted, slender, brownish tendrils.

The number of galls on cedar trees varied tremendously. Certain trees were apparently immune while others near at hand had but a few galls or were literally loaded with them. A branch twelve inches in length from a heavily infected tree was found to bear two hundred and fifty galls of various sizes. The size of the galls and the number of telia they produced also varied widely. The smallest galls were but two to three mm. in diameter and produced one or two telia only. Average-sized galls measured two to three cm. in diameter and produced from seventy to one hundred telia. A large-sized gall measured five and one-half cm. in diameter and produced three hundred and forty-seven telia.

Gelatinization and drying of the telia usually occurred six to eight times during a season, but by the middle of June most of the telia had dropped from the galls, after which both the galls and the fungus died. It frequently happened, however, that the galls remained on the tree in a more or less blackened and mummified condition for several months; occasionally the dead telia adhered also. In rare instances certain of the smaller galls resumed growth for a second season. In plates 96 and 97 are shown galls and telia of *G. Juniperi-virginianae* in various stages of development.

2. Histological Symptomatology—(a) on Pomaceous Hosts.

The histological symptomatology on the pomaceous hosts was very similar in all of the infected tissues. In the following account the more nearly average symptoms and signs will be described and attention will be called to any irregularities that were observed.

In the leaves of the apples the earliest observed sign of infection was the presence of hyphae among the palisade and mesophyll cells. Shortly after invasion of the tissues by the mycelium, protoplasmic symptoms of disease were observed as globules of deep-staining material in the infected cells. From six to ten days after inoculation densely intertwined masses of hyphae, the spermogonial primordia, were observed in various stages of development between the palisade layer and the upper epidermis. These primordia developed to mature sper-

mogonia by the fifteenth to twentieth day. During this interval the mesophyll cells increased slightly in size but seldom sufficiently to fill all of the intercellular spaces. The mycelium also increased in amount and occupied a greater area, as was evidenced by microscopic examination and the increase in size of the yellow discolorations on the surface of the leaves. During maturation of the spermogonia hyphae were observed to have formed haustoria in many of the parenchymatous cells. The haustoria were variable in size and shape, as shown in the camera lucida drawings in plate 94 fig. 7. Usually but a single haustorium was found in a cell; occasionally, however, two or three were observed.

Following the maturity of the spermogonia the mesophyll cells increased greatly in size and number and completely obliterated the intercellular spaces. The hypertrophied cells elongated at right angles to the surface of the leaf and forced the lower epidermis outward. From forty to sixty days after inoculations were made, compact masses of mycelium were formed just beneath the palisade layer in the hypertrophied mesophyll tissue. These masses of hyphae, the aecial primordia, elongated towards the lower epidermis. The central hyphal cells of the primordium gradually disintegrated and within this space the aecium was formed. From sixty to seventy days after inoculating, the aecia penetrated the lower epidermis of the leaf. One to three days later the peridial cells of the aecium separated along their sides, turned outward in characteristic fashion and released the aeciospores. A cross-section of a leaf at the border of an infected area is shown in plate 94, fig. 1. It is evident from this photomicrograph that the swelling of the leaf was due entirely to the elongation of the parenchymatous cells of the mesophyll tissue. In many instances it is clear that the mesophyll cells divided one to three times. Very little morphological change was observed in the palisade cells or in the upper or lower epidermis.

In the fruits the mycelium developed somewhat differently than in the leaves. Instead of being localized as was characteristic of leaf infections, the mycelium sometimes invaded the whole fruit. The infected parenchymatous tissue beneath the epidermis of the fruits responded to attack as did the mesophyll tissue of the leaf. In the smaller fruits the histological changes were observable almost to the core, but in the larger fruits histological changes extended over a portion only of the tissues. The spermogonia developed immediately under the epidermis of the fruit and appeared in all respects similar to those on the leaves. The aecial primordia were located about three

mm. below the epidermis, and upon reaching maturity penetrated the surface of the fruits among the spermogonia. In the twigs the fungus and the disease developed essentially as in the fruits.

In certain of the more susceptible species of *Malus*, buds of the current and the following season occasionally became infected and the embryonic tissues were forced. Within these tissues the symptomatology was somewhat different than in localized infections. The mycelium invaded all but the vascular tissues of the leaves, petioles and stem. Fructifications developed and matured progressively from the bases of the infected organs to their tips. Thus in a leaf while spermogonia were forming on the blade others were maturing nearer its base; these in turn were followed by developing aecia on the base of the leaf and by mature aecia on the petioles. The infected organs were greatly hypertrophied and showed histological changes similar to those already described. In the leaves, however, the mesophyll cells were much less hypertrophied than those in the localized infections; and the intercellular spaces were large and numerous. An unusual character of leaves of forced buds was that the tomentum, when present, remained constantly attached to the epidermal cells. The leaves on these buds usually adhered throughout the winter in a blackened condition. The forced buds and the portion of the twig or branch beyond them were killed, in all cases observed, during the winter. I have never observed the aecial phase of *G. Juniperi-virginianae* to overwinter.

In plate 95 are shown several photographs of forced buds in various stages of development.

2. Histological Symptomatology—(b) on Red Cedars.

The earliest symptoms of disease seen consisted of but a few enlarged parenchymatous cells in the leaves only of red cedars. The infected cells gradually increased in size and in number and produced globose swellings or galls on the leaves. During this development the vascular system of the leaves was also hypertrophied and ramifications were present throughout the galls. At maturity the galls varied in size from two to forty mm. in diameter and were covered with a thick epidermis of cork cells. In concave depressions just beneath the epidermis, the cells of the galls seemed to be retarded in their development. Within these areas the mycelium formed stromata of several compact layers of hyphae and from these the telial fructifications were developed.

The protoplasmic contents of the cells of the galls contained many small, deep-staining globules similar in many respects to those in the infected cells of the apple leaves. Certain of the cells of the galls,

however, seemed to be completely filled with a fine, granular, deep-staining substance.

3. Range of the Diseases Caused by G. Juniperi-virginianae.

At the present time, the diseases caused by *G. Juniperi-virginianae* have been reported from all but Arizona, California, Idaho, Nevada, Oregon, Utah and Washington in the United States and from Ontario only in Canada. In figure 1 is shown the distribution of the disease as dots on an outline map of North America. While the present range of the cedar-apple rust disease is delimited within the coinciding ranges of the pomaceous and Juniperus hosts in eastern North America, it must be borne in mind that host relationships are favorable for the organism over the greater part of western as well as eastern North America. The alternate hosts in eastern and western North America are separated from each other geographically by the great plains region of central North America.

Figure 1. Geographical distribution of

(a) the pomaceous hosts of *G. Juniperi-virginianae* is shown as vertical lines.

(b) the *Juniperus* hosts (exclusive of the doubtful *J. communis*) is shown as horizontal lines.

(c) *G. Juniperi-virginianae* is shown as dots.

It will be noted that the fungus is abundant over the coinciding ranges of the apples and eastern red cedars in eastern North America, but has not been reported on apples or the western red cedars in western North America. The great plains region separates these two groups of alternate host plants.

VI. LIFE HISTORY STUDIES OF G. JUNIPERI-VIRGINIANAE

Schweinitz (1822) described *G. Juniperi-virginianae* from the telial phase found on red cedars in North Carolina. This was the first species of the genus *Gymnosporangium* to be described from North America. Link (1825) described the same species as *G. macropus*, a name that was given preference over the former by many of the earlier writers. According to the 1910 rules of botanical nomenclature, however, priority is given to the name *G. Juniperi-virginianae*. Schweinitz (1832) described the aecial phase of this rust from material on *Malus coronaria* as *Caeoma* (*Aecidium*) *pyratum*.

In 1875 Professor W. G. Farlow working at the Bussey Institution of Harvard University attempted for the first time (as far as can be ascertained) in North America to culture a rust fungus. Professor Farlow sowed basidiospores of *G. Juniperi-virginianae* on leaves of two small plants of *Amelanchier canadensis*, but without positive results. It was not until the cultural studies of Halsted (1886) and Thaxter (1887) that *A. pyratum* and *G. Juniperi-virginianae* were shown to be genetically connected.

From his extensive cultural studies of several species, Thaxter summarized the life history of *Gymnosporangia* in general. "The *Gymnosporangia* on cedars produce spores (teleutospores), and these in turn produce sporidia which, falling on various *Pomeae*, result in the formation of *Roestelia*, producing aecidial spores, which serve to reinfect the cedars with *Gymnosporangia*." Thaxter further stated that the aeciospores of *G. Juniperi-virginianae* were about 25 μ in diameter and that the peridial cells were "about 22 μ x 80 μ and are marked by striae running obliquely and anastomosing obscurely, the outline of the cell being broken by coarse ridges. The cells when isolated tend to become curved outward—a fact to which is due the outward curling of the peridial lacerations." From his cultures on *M. pumila* (*M. Malus*) Thaxter found that the spermogonia appeared on spots on the upper surface of the leaves in about twenty-two days after inoculating and that aecia reached maturity on the lower surface in about seventy-one days.

Pammel (1905) stated that "The first appearance of the fungus upon wild crab is an orange patch varying from one-sixteenth to one-quarter of an inch across or occasionally somewhat larger." and that "the spermogonia make their appearance in from ten to eighteen days after inoculating."

Heald (1909) reported that the "rust shows first on the upper surface of the leaves as pale yellow spots about the size of a pinhead.

These spots begin to show a week or ten days after the 'cedar apples' have been in the gelatinous condition." Heald also noted an increase in the size and depth of color of the infection spots with age. "In a few weeks after the appearance of the spots, minute pustules appear in the center of each, and these later show as small black specks. These black specks represent the openings of the pycnia—which are flask shaped structures sunken in the tissues of the host." Heald described the aecia as occurring on cushions or blisters one-quarter to one-half inch in diameter immediately beneath the spermogonia.

Kern (1912) gave measurements of the aeciospores of *G. Juniperi-virginianae* as 16 to 24 μ x 21 to 31 μ and the peridial cells as 10 to 16 μ x 65 to 100 μ.

Reed and Crabill (1915) reported that the spermogonia reached maturity in about one month after infection. "The spermogonia are formed immediately beneath the epidermis of the leaf. A dense mass of short-celled mycelium collects at this point and grows until a size of about 130 x 120 μ is obtained. As development goes on the mycelium is seen to arrange itself in strands approaching a point at the apex which is to be later the ostiole. No distinct wall is present in the spermogonium, the strands which give rise to the spermatia being continuous with the strands which ramify between the host cells. At maturity the spermogonium ruptures the overlying epidermis, the fungus strands are somewhat protruded, and by abstriction the spermatia are cut off from these strands. The spermatia are thus continuously produced as are the conidia of mildews, until all of the mycelium of the spermogonium is used up and only a hollow space remains under the epidermis. The spermatia are ovate to club-shaped and measure 2 x 6 μ. Repeated attempts to germinate these spores have failed." Reed and Crabill also state that the mycelium is very similar to that in the cedar gall, but that it is uninucleate in the leaf. They found that the haustoria are "filamentous, much contorted and exist in the palisade cells and the spongy parenchymatous cells." These authors also reported that "the aecidia are initiated by the collection of a globular mass of mycelium in the hypertrophied spongy parenchyma immediately beneath the palisade layer. This mass gradually enlarges and elongates toward the lower epidermis as the aecidiospore chains lengthen. Meanwhile the outermost aecidiospores are differentiated to form peridial cells." They found also that the spermogonia and aecia in the fruit were identical with those in the leaf.

Liu (1933) reported that the mycelium in the apple leaf became very indistinct during formation of the fructifications, but that it was clearly visible at other times.

Many workers have contributed information on the germination of the aeciospores of *G. Juniperi-virginianae*, but to date this phenomenon is little understood. Heald (1909) found that the aeciospores germinated best in July and August in Nebraska. Reed and Crabill (1915) found it impossible to obtain germination of the aeciospores. Weimer (1917) obtained 25% to 75% germination on two tests, but 0% to 1% germination on many other trials. Thomas and Mills (1929) stored the aeciospores for eight weeks at 3°C. and obtained 80.5% germination. Miller (1932) periodically tested the germinability of overwintered aeciospores and found an increase in germination up to March 1929 and up to January 1930. The maximum germinations were 84% and 46% respectively. Bliss (1933) found that refrigeration greatly increased germinability; "the spores showed 16.8% germination when collected (July 28), but after the lot was divided the percentage germination in the refrigerated portion increased rapidly for at least twenty-two days, while that held at room temperature for the same interval dropped to zero." "These results suggest that aecidiospores of *G. Juniperi-virginianae* may infect red cedars when liberated from the aecidium but that refrigeration will increase and prolong their germinability."

No studies, however, have yet been made, so far as can be ascertained, regarding the infection of leaves of red cedars by aeciospores of *G. Juniperi-virginianae*. We are also at a loss to know when or under what conditions infection occurs. However, the telial or diploid phase of this organism in red cedars has received much attention and many interesting phenomena have been brought to light.

Farlow (1880) stated that the telial "mycelium of *G. Juniperi-virginianae* (*G. macropus*) is abundant and easily seen. It is found principally in the leaves and there are haustoria that enter the parenchymatous cells.—In some cases, the gelatinous columns are produced when the knots are quite small." The former "arise a short distance below the surface" and "by growth of the gelatinous masses the columns arise vertically." Lloyd and Ridgway (1911) found that during each of several rains the gelatinous masses elongated by further development of the sori in the gall. Reed and Crabill (1915) stated that the mycelium is "found occupying a portion of the intercellular spaces between the parenchymatous cells. The mycelial threads ramify throughout the cedar apple and grow for the most part closely appressed to the walls of the host cells." Haustoria were found only in the parenchymatous cells; they were "uniformly club shaped."—"The production and development of haustoria is very slow during the

summer, autumn and early winter, and in March just prior to the production of teleutospores haustoria were in great abundance." These authors also stated that "the first step in development of teleutospores is the formation of a compact mass of much-branched short-celled mycelium just beneath the cortex. This condition first becomes apparent about sixteen months after infection of the cedar leaf, that is, in the second December of its development. A layer of erect rectangular cells arise from this mycelial mass just beneath and perpendicular to the cortex. These cells elongate and their tips take on gradually the character of incipient teleutospores.—Soon after the teleutospore becomes recognizable as such the two nuclei in each cell fuse, the walls become much thickened, the stalk cell rapidly elongates into a pedicel and the spore is thus carried upward."

Dodge (1918) found that hyphae were in much greater abundance in the regions just beneath the depressions. "The upper cells grow against the cork layers and become somewhat flattened but they are usually slightly longer than the cells beneath.—The buffer cells finally become two or three times their original length and contain a thin watery substance that is lightly colored with orange G. Their walls become thinner and thinner and finally disappear altogether. After the buffer cells have lost their contents the cells below bud out, their nuclei move up to the base of the bud and divide.—A septum is formed at once. The young binucleate teleutospore bud grows comparatively slowly so that these stages are fairly abundant at the center of the young sorus. Buds may push out of the sides of the basal cell and later three or four buds may be formed from one cell."

Several workers have observed different types of germination of the teliospores of *G. Juniperi-virginianae* and other species of the genus. Heald (1909) working with *G. Juniperi-virginianae* stated that "when germination takes place with a minimum amount of moisture, the promycelium will be short and compact but with an increase in the water supply, a more elongated growth results." Coons (1912) working with this same fungus found that "in air that is partly exhausted of oxygen the germ tubes grew exceedingly long, eight to ten times their normal length, but produced no sporidia. In all cases when returned to air, spores were formed." Reed and Crabill (1915) reported that "an attempt was made to germinate normal teleutospores and sporidia in an atmosphere of carbon dioxide. The spores were suspended in water and incubated for five hours at 18° to 20°C. in an atmosphere of carbon dioxide. No germination took place. They were then incubated for twelve hours in air. Seventy-five percent of

the teleutospores germinated and about fifty percent of the sporidia. After twelve hours exposure to carbon dioxide, sporidia would not germinate under optimum conditions. Oxygen is apparently necessary for the germination of the teleutospores and sporidia." Weimer (1917) stated "these abnormal conditions of germination are usually found where an overabundance of moisture is present or where the temperature is somewhat below the optimum." Miller (1932) found that "an abnormal type of spore germination occurred in high temperatures, in which promycelia were formed, but no basidiospores were developed." Fukushi (1925) working with *G. Yamadae* in Japan, Barclay (1890) studying *G. Cunninghamianum* in India and Blackman (1904) using *G. clavariaeforme* in England, found similar behaviors in the germination of the teliospores and were of the opinion that those teliospores that germinated in an abundance of water usually produced long promycelia.

Many workers have noted the production of secondary basidiospores from the primary basidiospores developed on the basidium. Farlow (1886), Thaxter (1887), Crabill (1913), Reed and Crabill (1915), Weimer (1917) and Miller (1932) have observed this phenomenon. Reed and Crabill (1915) stated "indications are that when kept continually moist from the time of production, the primary sporidia will produce secondary sporidia and that when the primary sporidium becomes dry immediately following its production and subsequently wet, it may germinate either directly or indirectly. The extent of dryness may be the determining factor." Miller (1932) stated that the production of secondary basidiospores could be brought about at will by high temperatures and an abundance of water.

Reed and Crabill (1915) have made some interesting observations on the longevity of the basidiospores of *G. Juniperi-virginianae*. Basidiospores were collected on clean glass slides and kept air dry in the laboratory at a temperature of 15° to 21°C. and were tested daily for germination. They concluded that "five or six days is their life limit in an air dry condition."

Considerable variation was found in the reports on the time required for the production of basidia and basidiospores and the optimum temperatures at which the teliospores and basidiospores will germinate. Heald (1909) stated that "under favorable conditions the promycelium will be produced and the sporidia matured in twelve to twenty-four hours." Fulton (1913) found that from the first swelling of the gelatinous horns to the formation of the infection spores "about 24 hours of moisture were required." Reed and Crabill (1915) observed

that a minimum of four hours was required for the production of the promycelium. Weimer (1917) stated "on one occasion a spore taken from a telial horn had formed a small bud-like process at the end of one hour; after two and one-half hours the promycelium had continued its development and the septa were visible; by the end of three and one-half hours the basidiospores were formed."

Several workers have determined the minimum, optimum and maximum germination temperatures of teliospores and basidiospores of *G. Juniperi-virginianae*. The results of some of these are given below.

		Teliospores			Basidiospores		
Investigator		Min.	Opt.	Max.	Min.	Opt.	Max.
Reed and Crabill	1915	11.5°C.	15°C.	29°C.	8°C.	13°C.	24°C.
Weimer	1917	7°C.	22-25°C.	29°C.			
Miller	1932	4°C.	24°C.	32°C.	8°C.	16°C.	28°C.

Certain workers have reported finding teliospores of *G. Juniperi-virginianae* that germinated with the production of two or three basidia for each cell. Among these may be mentioned Farlow (1880) and Lloyd and Ridgway (1911). It is the finding of other workers, however, that each cell of the teliospore produces but a single basidium.

Little work has been done on the infection of apple leaves by basidiospores. Coons (1912) observed the germination and penetration of germ tubes into apple leaves. He stated that "it was possible to see the hyphae from the sporidia after a vagrant, tortuous growth in the water, bend sharply downward at the edge of the drop and pass into the cell beneath." Coons also noted that "an elongated sterigma penetrated the cuticle of the host directly." Coons inoculated the upper surface of the leaves of one group of apple seedlings and the lower surface of another group. Greater amount of infection resulted from the inoculations made on the upper surface. Weimer (1917) gave an illustration in his figure 141*e* which was described in the text as a germ tube penetrating a cell of the lower epidermis.

To the life history studies as reviewed in the foregoing, I can add little that is new. In the following account of my own work on the aecial phase of *G. Juniperi-virginianae* further studies have been made on certain phenomena and the past and present results are compared and correlated with respect to the relative susceptibility of hosts in the genus *Malus* other than the orchard apples. My own work on the telial phase of this rust includes field observations on the development of the fructifications in Massachusetts as well as laboratory studies on the formation, germination and longevity of the teliospores.

The galls of *G. Juniperi-virginianae* were found to bear numerous yellowish-brown gelatinous telia in April, May and the early part of

June in Massachusetts. During rains of this period the telia absorbed much water and swelled to several times their former volume. When the telia were gelatinized the teliospores germinated and produced vast numbers of basidiospores or sporidia. The basidiospores were wind borne and those that chanced to alight on susceptible parts of pomaceous hosts may have germinated in one to three hours and infected the host and initiated the haploid phase of the rust.

The mycelium of this phase was always clearly visible when stained with the safranin-haematoxylin dyes. It was found among the palisade and spongy mesophyll cells of the leaf and among the cortical cells of the fruits and twigs. The mycelium was uninucleate, 1.5 to 2.5 μ in diameter, and irregular in contour, septate and much branched. It remained localized in the infection areas and increased in amount, up to a certain limit, with the age of infection. From seven to ten days after inoculations were made small discs of mycelium were seen in microscopic section between the upper epidermis and the palisade layer. These discs increased rapidly in all dimensions, and in one to three more days certain of the hyphae at the center of the primordium became apically directed and seemed to act as buffer cells as described by Miss Allen (1930, 1932). These buffer cells seemed to aid in raising the epidermis and at the same time possibly also aided in the increase in diameter of the young spermogonium. The buffer cells soon lost much of their protoplasm and the property of staining deeply with safranin. They stained very lightly in contrast to the heavily stained peripheral hyphae. During and following the loss of their protoplasm the buffer cells also became greatly disintegrated. Deep-staining elongate cells, the spermatiophores and possibly the paraphyses also, were seen pushing towards the center and from the sides and base of the spermogonium. Before the complete disintegration of the buffer cells and most frequently before the ostiole was formed, spermatia were being abstricted from the tips of the spermatiophores. In plate 92 are shown photomicrographs of developing spermogonia.

In leaves of the moderately susceptible species of Malus spermogonia reached the stage of oozing or maturity in from ten to twenty days after inoculations were made. In the more resistant hosts the time required to reach maturity was progressively longer as shown in table II. In the most resistant hosts the spermogonia were seldom observed to have oozed, although they were examined every three days during the entire summer.

At maturity the average size of the spermogonia was 183.7 μ in height by 190.2 μ in width and they were sunken 109.0 μ beneath the

epidermis of the host. The spermogonia of *G. Juniperi-virginianae* is of great diagnostic value. No other in the genus is like it in shape and size. A full account of the morphology of spermogonia of all the species of *Gymnosporangium* is in preparation.

The duration of oozing of the spermogonia varied from a few days to many weeks. The average period of oozing of spermogonia was from seven to ten days, but under certain conditions, particularly in isolated infections, spermogonia continued to ooze for upwards of a month or even longer. Microscopic examination of infected areas on which spermogonia continued to ooze for long periods showed that young spermogonia were being produced among those already dead. Upon the death of the spermogonia they were completely plugged with hyphae and they usually turned black.

The spermogonial exudate of *G. Juniperi-virginianae* had a distinctly sweetish taste. It attracted certain insects. Both red and black ants were often seen swarming over the infected leaves seemingly drinking the nectar. It was interesting to lightly tap a leaf on which the insects had been present for some time. Usually they behaved as if intoxicated; they easily lost their balance, experienced difficulty in getting up and walked aimlessly about. They generally seemed quite contented, however, when they again found an exudate droplet. Thaxter (1887) reported "that small flies were repeatedly observed feeding on the secretion of the spermogonia."

Following the maturity of the spermogonia the mycelium increased vegetatively and occupied wider areas in the infection spots. From forty to fifty days after inoculating irregular yet compact masses of hyphae were observed in the hypertrophied leaf tissue just beneath the palisade layer. With further development these masses of hyphae, the aecial primordia, elongated at right angles to the surface of the leaf. When the primordia reached a certain size the hyphae in the central portion began to disintegrate. From the base of the primordium short-celled binucleate hyphae were seen to grow into the disintegrating tissues. These hyphae soon developed to a plate of regular cells, the hymenium of the aecium. The central cells of the hymenium at first gave rise to peridial cells which penetrated into the disintegrating tissues as a cone of thick-walled cells. Following the production of peridial cells the central hymenial cells gave rise to aeciospores only while the peripheral hymenial cells continued to give rise to peridial cells. These peridial cells joined up with those already formed, that is, the terminal ones, and thus completed the peridium surrounding the aeciospores.

On an average of sixty to seventy days after inoculating, the aecia penetrated the lower epidermis of the swollen cushion and protruded as short acuminate cylinders. In one to three more days the peridium split open and the chains of peridial cells turned outward in characteristic fashion, releasing the aeciospores. The aecia of *G. Juniperi-virginianae* are easily differentiated from most species of the genus, as those of the cedar-apple rust fungus are of the *Aecidium* type. Most other species of *Gymnosporangium* have aecia of the *Roestelia* type which first open irregularly along the sides in cancellate fashion. The peridial cells of this and other species of *Gymnosporangium* are of much diagnostic value as was pointed out by Fischer (1891) and Kern (1910).

The time of maturity of the aecia and the duration of aeciospore production are phenomena that vary directly with the relative susceptibility of the host upon which the parasite is growing. From table VII it will be seen that the aecia reached maturity most rapidly on the most susceptible hosts, and that progressively longer periods were required for the maturity of aecia on the more resistant hosts. The duration of aeciospore production is probably a related phenomenon. In the more resistant hosts the infection spots and the mycelium usually died before the leaves fell. In the very resistant species, *M. fusca* and *M. sylvestris*, many of the infection spots and the mycelium also died early in September in 1932 and 1933. With the death of the mycelium aeciospore production ceased. In the more susceptible hosts most of the infection spots lived and aeciospore production continued throughout the growing season. In the most susceptible hosts, however, aeciospore production continued on many of the infection spots even after the leaves and fruits were picked. On September 24, 1933, leaves and fruit of several of the most susceptible hosts were gathered for the purpose of overwintering the aeciospores. In November and December when these were examined many of the aecia had elongated and aeciospores were clustered in masses about the sori. It was observed, however, that aeciospores were produced most abundantly on the fruits, and only on those leaves that were still green and apparently quite healthy at the time of picking. Thomas and Mills (1929) reported observing this phenomenon on picked apple fruits.

The aeciospores of *G. Juniperi-virginianae* averaged 25.4 μ by 22.0 μ with extreme measurements of 33.0 to 19.8 μ x 26.4 to 16.5 μ. In mass, aeciospores were auburn in color as was determined from Ridgway (1912).

Aeciospores of *G. Juniperi-virginianae* germinated only 1 to 3% in the summer. When gathered in September, 1933, and overwintered in cheesecloth bags they showed only a slight increase in germinability up to January, 1934, and practically no germination thereafter. The aeciospores of this rust are wind borne. They are distributed throughout the summer and many of them must become lodged on the leaves of red cedar trees. No evidence of infection is visible, however, until galls begin to form on the needles of red cedars in June and July of the following spring.

In red cedars the mycelium of the telial phase of *G. Juniperi-virginianae* is found in the infected needles and galls that they bear. The hyphae are binucleate, 2 to 3 μ in diameter, septate and much branched. With increase in the size of the galls the mycelium invaded the new tissues and was found in abundance around all but the epidermal cells. During its vegetative activities the mycelium formed haustoria in adjacent host cells. The haustoria were simple, unicellular, sac-like cells usually with but a single nucleus, but occasionally with two. In plate 98, fig. 5, are shown camera lucida drawings of haustoria of this phase of the rust.

Towards the end of the summer, about August or September in Massachusetts, reproductive activities of the mycelium were first manifested. Beneath each concave depression on the surface of the gall the mycelium formed a stroma of several layers of small, nearly cubical cells. From the stroma a sorus of teliospores was produced. My results agree in detail with those of Dodge (1918) regarding the formation of the teliospores of *G. Juniperi-virginianae*. The uppermost cells of the stroma elongated to several times their former length and lost much of their contents. From the sub-terminal cells a slender hypha was sent into each elongated or buffer cell. These slender hyphae differentiated into teliospores and stalks, as is shown in plate 98, fig. 2. Usually two or three teliospore initials were formed on each sub-terminal cell. These were produced as lateral branches and were not formed within buffer cells. Teliospore formation began near the center of the sorus and progressed peripherally. Thus, spores in all stages of formation could be found at the periphery of the sorus at the base of the telium.

Certain morphological and physiological phenomena of the teliospores are of considerable interest. The wall thickness of 424 teliospores was measured; the measurements fell into three groups, namely, (a) 1 to 1.5 μ thick, 191 spores, (b) 2 to 2.5 μ thick, 49 spores, and (c) 2.5^{+} μ thick, 184 spores. From these results it is seen that the

thick—(2.5+ μ) and thin—(1 to 1.5 μ) walled spores are about equally abundant and that about 15% of the spores have an intermediate wall thickness. Of 1117 teliospores counted from several telia, 1000 or 90% were two-celled and 117 or 10% were one-celled. With rare exception the unicellular spores were thick-walled. Microscopic examination showed that the preponderance of thick-walled spores (both one- and two-celled) was located in the outermost layers of spores in the telium; the inner spores were only thin-walled.

The topographical distribution of the germ pores in the apical cell of the teliospore was also studied. The upper cell had its germ pores either laterally near the septum and one to three were present, or a single germ pore was located at the apex. Rarely was a cell found that had germ pores in both positions. In a count of 310 teliospores, 220 or 71% possessed lateral germ pores, while 90 or 29% possessed apical germ pores. In the basal cell of the teliospore one to three germ pores were located, with rare exceptions, near the septum.

Measurements were made of the top cell, the basal cell, the total length and the width of fifty two-celled teliospores. The measurements were: top cell, 18.8 to 30.0 μ, average 25.4 μ; basal cell, 18.8 to 33.0 μ, average 23.9 μ; total length, 42.9 to 61.0 μ, average 49.3 μ; and width, 16.5 to 23.1 μ, average 18.2 μ. The total length and width of fifty unicellular teliospores measured 33.0 to 49.5 μ × 13.5 to 19.8 μ, average 40.8 μ × 15.2 μ. The unicellular teliospores resembled the two-celled ones in all but the cross wall.

The number of teliospores produced on an average-sized telium is impressively large. An estimation may be obtained by simple mathematical calculations. The average dimensions of a cylindrical telium were found to be 4 cm. long by 4 mm. in diameter, and the two to four (two to be conservative) peripheral layers of teliospores in close contact measured on the average 49.3 μ × 18.2 μ. Calculations showed the number of teliospores in a single telium to be about 22,300,000. The number of basidiospores is naturally many times greater, theoretically up to eight times as many. Thus a single small gall bearing six telia (an average number for a small gall) produces about one billion basidiospores, an average-sized gall with fifty telia about eight billions, and a large gall upwards of sixty billions.

For the purpose of testing the effect of water and air on the germination of teliospores of *G. Juniperi-virginianae,* telia were first wetted in water and placed on dry glass slides in a moist chamber and examined *in situ.* Those teliospores next to the slides were naturally wholly immersed in water and so excluded from a ready supply of air, while those not in contact with the glass were covered by a thin film of water

only and so were more accessible to air. Many of the teliospores that were immersed in water produced long germ tubes, while the others developed both basidia and basidiospores.

It has been the writer's experience to find that teliospores from young telia produced basidiospores within three to four hours; but as the telia aged the time required for germination of the older spores increased. The time required for germination of teliospores kept in a refrigerator was determined. In October approximately eighteen hours were required for the production of basidiospores, while in February only a small percentage of the teliospores germinated at the end of thirty-six to forty-eight hours and a few of these produced basidiospores.

After the production of one crop of telia the gall and the mycelium in it usually died. Rarely, however, the growth of the gall and the mycelium were continued and a second crop of telia was produced. In plate 97, fig. 2, is shown a small gall of *G. Juniperi-virginianae* that produced one crop of telia and survived for another season. In plates 96, 97 and 98 are shown photographs and drawings of galls and telia in various stages of development.

VII. BIOLOGICAL STRAINS OF G. JUNIPERI-VIRGINIANAE

Several workers have cultured *G. Juniperi-virginianae* from various localities upon a few species of *Malus*, including several varieties of orchard apples, but their findings are not in harmony.

Stewart and Carver (1895) obtained telial material of *G. Juniperi-virginianae* from Iowa and New York and made cultures on varieties of orchard apples. They found that on most of these the fungus developed essentially the same. A slight difference was reported, however, for Red Pippin—no aecia were produced by the fungus from Iowa, but aecia were partially developed by the fungus from New York. Pammel (1905) found no biological strains in telial material from Missouri and Long Island, New York. Arthur (1905) found no difference in the rust from North Carolina or Iowa when cultured on orchard apples. Weimer (1917) cultured the rust from Nebraska, West Virginia and New York on Wealthy apples in the open and on seedling apples in the greenhouse. "In no case was there any evidence to show that one strain was more virulent than the other." Bliss (1928, 1933) on the other hand, showed that biological strains existed within the state of Iowa. He also found biological strains from Kansas, West Virginia, New York, Wisconsin and Ontario.

In order to further investigate this phenomenon, inoculation experiments were made on forty-five species of the genus *Malus* in the

Arnold Arboretum in the season of 1933. Telial material of *G. Juniperi-virginianae* was obtained from eight localities in the United States, namely, Alabama, Kentucky, Massachusetts, Michigan, Missouri, Nebraska, New York and West Virginia. All of the inoculations were made early in the growing season and within a period of one week. The results showed marked differences in the virulence of the parasite from each of the eight states. According to my results biological strains of *G. Juniperi-virginianae* do exist. The data are presented in table VII. The aecial hosts are arranged in order of decreasing

TABLE VII.

RESULTS OF THE INOCULATIONS ON THE POMACEOUS HOSTS IN THE GENUS MALUS WITH G. JUNIPERI-VIRGINIANAE FROM EIGHT STATES—A TABULATION OF THE NUMBER OF DAYS REQUIRED FOR THE DEVELOPMENT OF THE AECIA

	Mass.	Nebr.	Mich.	N. Y.	Mo.	Ky.	Ala.	W. Va.	Averages
MALUS									
ioensis plena	52	h	61	53	61	60	lost	dd	59
Soulardi	52	h	h	53	h	64	64	70	60
coronaria	56	60	65	60	lost	61	64	68	62
lancifolia	56	60	61	59	68	dd	66	65	62
angustifolia	56	61	64	63	56	68	66	69	63
glaucescens	56	62	60	59	62	69	65	71	63
platycarpa	63	60	61	59	66	66	70	68	64
glabrata	63	60	62	64	dd	00	71	72	65
bracteata	59	62	64	67	76	lost	dd	74	67
ioensis	60	h	h	63	h	69	70	76	68
Dawsoniana	69	00	00	76	00	00	00	00	72
sylvestris	65	h	00	71	00	00	73	82	73
fusca	75	00	h	73	h	h	h	h	74
Averages	55	60	62	63	65	65	68	70	

h — hypersensitive dd — inoculated branch died
00 — no infection resulted

susceptibility and the states are arranged in order of decreasing virulence of the parasite as indicated by the average number of days required for the maturity of the aecia. From this table it will be seen that the rust from Massachusetts matured its aecia in an average of 55 days and that the fungus from the other states required progressively longer periods; that from West Virginia required the longest time, namely, 70 days. It will also be observed that the rusts from Massachusetts and New York were the only ones to parasitize all of the aecial hosts. The strains from Nebraska, Michigan and Missouri failed to produce aecia on *M. fusca, M. sylvestris, M. Dawsoniana, M. ioensis* and *M. Soulardi.* It is of interest to note that the hybrid *M. Soulardi* (*M. ioensis* × *pumila*) reacted to infection by the rust from each of these states, as did the susceptible parent *M. ioensis.* The hybrid *M. Dawsoniana* (*M. fusca* × *pumila*) was parasitized only by the same rust strains as was the susceptible parent *M. fusca.* In *M. fusca,* however, the rust strains usually produced infection, but the rust and the infected areas died before the production of aecia. Likewise it is of interest to note that on the average (with one exception in each of the two hosts) the strains of the rust from each state produced aecia on the hybrids *M. Dawsoniana* and *M. Soulardi* in shorter time than on the parent species *M. fusca* and *M. ioensis.* The presence of biological strains of this fungus in various geographical areas may be an important factor in accounting for the variable reports on the relative susceptibility of orchard apples received from several states.

VIII. OBSERVATIONS ON FACTORS INFLUENCING THE AMOUNT OF INFECTION ON HOSTS OF G. JUNIPERI-VIRGINIANAE

The topic of this section is in part expressed by the term epiphytology as defined by Whetzel (1925), namely, "that phase in the study or discussion of a disease which deals with relation of environmental factors to its occurrence, severity and character. These factors are chiefly climatic, soil and cultural. They influence the disease indirectly through their influence on the pathogene or the suscept or both." But it is somewhat broader still because it includes factors inherent in the constitution of the host and in the pathogen. Undoubtedly the inherent constitutions of both the host and the pathogen have an important influence on the "occurrence, severity and character" of the disease. That this is so is shown by the results of the inoculations as recorded in table VII. The importance of external environmental

factors, however, is not minimized. The influence of factors of both kinds have been studied and I now pass to a description and discussion of the results observed. Greater strength is added to the exposition by including corresponding observations relative to various *Gymnosporangium* diseases other than those caused by *G. Juniperi-virginianae*. The findings herein reported are largely field observations made during the present investigation. In certain instances, however, examples by previous investigators are discussed and hypothetical cases are constructed from combinations of possibilities.

(A) Relation of the location of the source of inoculum to the amount of infection on Malus spp.

The location of the source of inoculum has a pronounced influence upon the amount of infection. Certain localities facilitate distribution of the inoculum, others hinder it. The transfer of inoculum is influenced by such features as distance, bodies of water, elevation of the source, intervening bodies and wind.

The distance that the inoculum must travel before reaching a host, if short, usually facilitates distribution of the fungus. Planting aecial and telial hosts in close proximity creates ideal conditions for the continuation of the rust when once established. Such plantings have been frequently met with in home gardens and on large estates. The same scheme has been carried out on an extensive scale in several of the midwestern states where red cedars are used as windbreaks around apple orchards.

Large bodies of water also are usually an advantage to the dispersal of the inoculum. Thaxter (1887) recorded an instance in which basidiospores of *G. biseptatum* Ellis infected chokeberries, *Aronia* sp., eight miles from the only source of inoculum known to him. The source of inoculum was infected branches of *Chamaecyparis thyoides* B. S. P. on an island off the coast of Maine. While my investigations were in progress, Mr. J. D. MacLachlan (who grants permission to report the observations made) found certain shad bushes and hawthorns that were infected with both *G. clavipes* and *G. globosum*. After an intensive search of the surrounding territory it was determined that the only source of inoculum was six to seven miles from the infected plants. The basidiospores of these rusts travelled chiefly over water and were probably aided by the greater humidity and the unobstructed area.

The height of the source of inoculum seems to favor a greater distribution of the fungus. Bartholomew (1912) described a case in

which susceptible apple trees were variously located with respect to a bluff on the top of which were infected red cedars, namely, (a) one group at the base of the bluff, (b) one group one-fourth mile distant, and (c) a third group one mile distant. It was determined that the percentage of infected leaves was 60%, 55% and 7% respectively for the three groups of apple trees. While the trees one mile distant were but 7% infected it is to be borne in mind that trees at that distance are generally presumed to be outside the range of distribution of the basidiospores of *G. Juniperi-virginianae;* this belief is reflected in the recommendations regarding cedar eradication, that is, that eradication for a radius of one mile protects apple trees. Unquestionably the greater range in the instance recorded by Bartholomew is related to the relative height of the inoculum.

Within limited distances, however, certain barriers may serve to confine the inoculum. Thus if red cedars harboring the inoculum are surrounded by taller trees the spores tend to be retained within a small area. A striking example of this is given by Giddings (1918). He described a large grove of infected cedars growing close to a row of susceptible apple trees. "A strong wind was blowing from this grove into the orchard at the time of infection, and the effects of the disease appeared to be at least twice as severe on the side toward the cedar grove as on the other side." From this example it seems that many basidiospores were lodged and so prevented from travelling through the trees. In my own investigations many similar instances have been observed. On the Lyman estate, Canton, Mass., two groups of red cedars and shad bushes were growing about two hundred yards apart. The red cedars and shad bushes in one group were heavily infected with *G. clavipes* C. & P., while the plants in the other group were heavily infected with *G. Nidus-avis* Thaxter. Both of these groups were surrounded by high cedars, beeches and pines. Enormous numbers of spores were produced each year on the heavily infected hosts in each group. The contagion, however, was held within the group and only occasionally did the inoculum from one group reach the other. Another example may be cited. In an old pasture off Trapelo Road, Waltham, Mass., two small groups of apple trees were surrounded by red cedars. The cedar trees were also abundant over the rest of the pasture. *G. Juniperi-virginianae* was unusually plentiful on the apple trees in each group. The nearest cedar trees were literally covered with galls. Progressively farther from the apple trees the number of galls on the red cedars rapidly decreased. At about one hundred feet distant only a few scattered galls could be found. This phenomenon seems to be due in part to the reduced carrying capacity of the wind

because of progressively decreased rates of travel through the trees and in part to the fact that branches and leaves of the barrier trees presented a large surface to which the spores could adhere, leaving fewer to be carried further. These two factors acting together are sufficient to account for the limited range of spore distribution in plantings that are surrounded by taller trees.

The direction of the wind at the time of spore production necessarily governs to a considerable extent the direction of spore dispersal. Apple trees that are in the windward direction are liable to receive a greater number of spores and thus may become more heavily infected than those in the leeward direction.

(B) The influence of age and wounds on liabiliaty to infection.

It has previously been shown that the leaves of many species and varieties of *Malus* are susceptible for a certain interval only during their youth. Because of the shortness of this period the less susceptible hosts are more protected by virtue of this phenomenon. As many of the orchard apples are only slightly susceptible, this fact assumes important, practical significance. Giddings and Berg (1915), however, noted that fully mature leaves of certain apple varieties sometimes became infected through insect injuries. Miller (1932) inoculated wounded and unwounded leaves of resistant varieties of apples. He obtained infection on only the wounded margins of the leaves. In my own work, fully mature leaves of *M. ioensis plena* that were quite past their period of susceptibility were cut in several places with a knife. Some of them were inoculated immediately. The next day more of the cut leaves and several of the uncut ones of approximately the same age were inoculated. Upon later examination it was found that those leaves that were cut and inoculated immediately became infected along the margins of the cuts but remained practically free from infection between the cuts. Those leaves that were not cut and those leaves that were cut one day and inoculated the next showed only slight evidence of infection. As a practical example, we may find hosts past their period of susceptibility that become infected after being wounded during rain storms in which basidiospores were dispersed.

(C) Influences of spring weather conditions on pomaceous hosts and on the telia of the rust.

In Massachusetts the telia of most species of *Gymnosporangium* appear about the first of April. The teliospores are germinable immediately or shortly after their appearance. Buds of most of the pomaceous hosts, however, do not appear until two to four weeks later.

The temperatures and the amount of rainfall during this period are very important. Should the rains be heavy and frequent, many of the teliospores will have germinated and come to naught because the susceptible parts of the alternate hosts are still enclosed in the buds. Should this period of wet weather be followed by a dry period, during which the buds open and pass their stage of susceptibility, little infection would probably result from subsequent rains. Warm rains between 15°C. and 24°C. when the buds are unfolding and the leaves expanding probably favor the fungus, as it has been shown that basidiospore production reaches a maximum between these temperatures.

The structure and development of the telium greatly influence teliospore production. It will be shown that the telium of *G. Juniperi-virginianae* adds a cylinder of fresh spores at its base during each of six or seven gelatinizations in the spring. The chances for successful infection by rusts with this type of telium is favored by the fact that the production of inoculum is distributed over a long period of time. This method of development seems to be restricted to species of *Gymnosporangium* with telia of the columnar type. Those species with low pulvinate telia, as *G. clavipes,* usually fully expose their sori after two or three rains. Although the spores do not all germinate at one time, nevertheless, by the end of two or three subsequent rains the telia have fully gelatinized and dropped from the branches.

(D) THE INFLUENCE OF HEALTH OF POMACEOUS HOSTS WITH REFERENCE TO THEIR LIABILITY TO INFECTION.

The health of pomaceous hosts seems to influence the amount and development of infection. In the Arnold Arboretum several small plants of *M. ioensis plena* were heavily infected with cedar-apple rust in the spring of 1931. That fall the trees were moved to a new location. The next spring they seemed to be in rather poor health. Both natural and artificial inoculations resulted in few and smaller than average infection spots. In the summer of 1933 the infection spots were larger and more numerous. In 1934 the infection spots were equally as numerous and fully as large as those on long established individuals of the same variety. From these limited observations it seems that the poorer health of the trees may account for the decrease in the size and number of rust spots.

(E) THE INFLUENCE OF THE PRESENCE OF MORE THAN ONE SPECIES OF GYMNOSPORANGIUM ON THE SUSCEPTIBILITY OF INFECTED PLANTS AND ORGANS OF MALUS SPP.

The presence of one species of *Gymnosporangium* does not exclude the possibility of other species growing on the same host or even on the

same organ. Many examples of more than one species growing in close proximity have been observed. *Gymnosporangium clavipes* and *G. globosum* were frequently found on the same individual of *Crataegus*. *Gymnosporangium Juniperi-virginianae* and *G. Nidus-avis* were successfully cultured on the same leaves of several species of *Malus*. Mature aecia of *G. clavipes* and *G. Nidus-avis* were sometimes found on the same fruit of *Amelanchier oblongifolia*. Many similar examples could be cited, but these will suffice.

Several phenomena have also been studied with relation to their influence on the amount of infection caused by *G. Juniperi-virginianae* on red cedars. These include the phenomena of sex, twig growth, presence of more than one species of *Gymnosporangium* and the duration of aeciospore production.

(F) The influence of sex of red cedars on infection by Gymnosporangium.

Reed and Crabill (1915) reported that many farmers were of the opinion that pistillate cedars only became infected with *G. Juniperi-virginianae*. After examining many trees of each sex—a total of two hundred ninety-three trees—they state that their notes "show conclusively that sex does not influence infection" of red cedars. In extending observations on this phenomenon, a survey of red cedar trees was made in areas around Boston where *G. Juniperi-virginianae, G. clavipes, G. Nidus-avis* and *G. globosum* were very common. Male and female trees were about equally abundant in these areas. The results show clearly that trees of each sex were attacked by each of these species of *Gymnosporangium*, and no preponderance of infection was noted for either sex.

(G) The influence of the presence of more than one species of Gymnosporangium on the susceptibility of red cedars.

Simultaneously with the foregoing survey data were recorded relative to each species of *Gymnosporangium* that was found on red cedar trees. In table VIII are presented data on this survey. The results show that nearly all possible combinations of the four species of *Gymnosporangium* were found on trees of each sex. Not only were two or more species of *Gymnosporangium* found on the same tree, but also several species were found growing on the same branch. Small branches of red cedar were frequently observed to be infected with galls of *G. Juniperi-virginianae* and *G. globosum*. Branches were also found with *G. clavipes* and one or both of these gall forms. A twig of *J. virginiana* was found on which two adjacent leaves were infected,

one with *G. Juniperi-virginianae*, the other with *G. globosum*. Perhaps the most striking instance of the close association of two species of *Gymnosporangium* was a small witch's broom caused by *G. Nidus-avis* that had on its twigs no fewer than fourteen galls of *G. Juniperi-virginianae*. From these observations it may be stated as a general principle that the presence of one species of *Gymnosporangium* does not necessarily exclude the possibilities of other species growing on the same tree or even on the same branch or twig.

TABLE VIII.

THE INFLUENCE OF SEX AND THE PRESENCE OF MORE THAN ONE SPECIES OF GYMNOSPORANGIUM ON THE SUSCEPTIBILITY OF RED CEDARS

Sex of red cedar	J-v	c	g	N-a	J-v,c	J-v,g	J-v,N-a	c,g	c,N-a	g,N-a
Female	15	1	0	0	1	6	14	5	0	0
Male	15	1	2	1	2	2	4	3	0	0
Undetermined	13	3	2	1	1	2	5	3	1	1
Totals	43	5	4	2	4	10	23	11	1	1

Continuation of table 8

J-v,c,g	J-v,c,N-a	J-v,g,N-a	c,g,N-a	J-v,g,c,N-a	Imm.	Totals
3	2	0	0	2	4	53
2	2	0	0	2	1	37
4	4	0	0	1	10	51
9	8	0	0	5	15	141

J-v — *G. Juniperi-virginianae* Schw.
c — *G. clavipes* C. & P.
g — *G. globosum* Farl.
N-a — *G. Nidus-avis* Thax.
Imm. — Immune.
The figures refer to the number of red cedars observed.

(H) THE DURATION OF AECIOSPORE PRODUCTION IN RELATION TO INFECTION OF RED CEDARS.

The number of aeciospores produced is largely governed by the size, the abundance and the rate of production of the aecium. Of the rate of production practically nothing is known. Observations have been made, however, on the comparative sizes of the aecia as well as on the duration of their activity. On very susceptible varieties as *M. ioensis*

plena and *M. coronaria Charlottae,* the aecia were relatively numerous and aeciospore production of *G. Juniperi-virginianae* continued throughout the growing season. In fact it was found that aeciospores continued to be formed even after vigorous leaves and fruit were picked in the fall. Thomas and Mills (1929) also observed this phenomenon on apple fruits. On the less susceptible hosts, however, the size of the aecia was smaller, their numbers fewer and aeciospore production continued for shorter periods. On *M. fusca* and *M. Dawsoniana,* for example, infection spots usually died and aeciospore production ceased early in September.

Another example of this phenomenon is shown in the case of *Amelanchier oblongifolia* and *Crataegus mollis,* both of which were about equally infected about the same time with *G. clavipes.* The fruit of *A. oblongifolia,* as is also true of other species of *Amelanchier,* ripened and dropped off about July 15, at which time aeciospore production ceased. The fruit of *C. mollis,* however, did not ripen until about September 1 and aeciospore dissemination continued throughout this time. Thomas and Mills (1929) have shown that aeciospore production of *G. clavipes* may continue on the fruits of apples even after they are picked. The fact that aeciospore production may continue after the leaves and fruit have fallen suggests at once the cultural treatment of destroying all infected litter under the trees as an aid to controlling the rusts.

IX. CONTROL OF G. JUNIPERI-VIRGINIANAE ON APPLES AND ON RED CEDARS

Heretofore, control of the cedar-apple rust disease has been concentrated almost exclusively on commercial orchards. Two methods have been tested, namely, control by the use of fungicides and control by eradication of red cedars. Investigations on fungicidal control measures have been fairly numerous but they have not been adopted, partly because experimenters failed to find satisfactory ones and partly because of the instant success that followed the eradication of red cedars. In spite of the fact that cedar eradication measures have been very successful such objections have been raised, in almost every region where eradication was attempted, as to defeat the efforts towards enforcement. At the same time little progress has been made toward working out and popularizing fungicidal control measures. Interesting as is this situation with regard to the present status of cedar-apple rust control in commercial orchards, the immediate stimulus of my own work as stated in the introduction of this paper, lay in demands for

information on the control of this fungus on ornamental apples and red cedars, a phase which has so far received little or no attention. In this connection, of course, red cedar eradication in most cases would automatically be ruled out. Naturally it is hoped that if this phase of the problem can be solved, adaptations feasible in commercial orchards will follow. An account of my work is prefaced by a brief review of the literature on control in commercial orchards.

1. HISTORY OF THE CONTROL OF THE RED CEDAR-APPLE RUST FUNGUS.

(a) Control by eradication of red cedars.

In 1888 Professor B. T. Galloway (1889), after observing the ineffectiveness of sprays to control *G. Juniperi-virginianae* on apple hosts wrote, "As a remedial measure it passes without further comment that it is well to destroy all specimens of the red cedar or savin." This is the earliest record found recommending the eradication of the red cedar.

Jones (1892, 1893) reported a practical test of eradication of red cedars. He stated, "In the fall and winter of 1891-1892, all the red cedars were destroyed in this (Vermont) orchard for a radius of one mile around. The results were magical. In former years, many of the trees were entirely defoliated by rust in August; the past summer not a rusted leaf was found in the entire orchard."

Reed, Cooley and Crabill (1914) recommended a cedar-free area of one-half mile around apple orchards in Virginia.

Giddings and Berg (1915) gave considerable data on the cost of eradicating red cedars in West Virginia; they came to the conclusion that "the actual cost of removing cedar trees for a radius of one mile around an orchard of six hundred or more susceptible trees would be equal to the fruit loss which might be expected to occur in one season as the result of a severe infection of apple rust." An area including 1,113 acres was cleared at an expenditure of $532.68 which was about 48 cents per acre.

Jones and Bartholomew (1915) strongly advised the removal of red cedars as the most certain and most practical means of controlling *G. Juniperi-virginianae* in Wisconsin.

Fromme (1918) made a strong appeal for the adoption of a cedar eradication law in Virginia. According to his estimates the cost of a single spray application in Frederick County (Virginia) in 1917 was about $3.00 per acre; while the cost of removing red cedars was shown to be about $2.50 per acre of apple trees. "As cedar eradication has been enforced in this county for four years," Fromme says, "the growers of Frederick County, if my figures are reasonably accurate,

have had four years protection from cedar rust at the cost of a single spray application." In oratorical language Fromme continues, "The question is often asked, 'Is there no spray for cedar rust?' Why in the world would anyone want to spray for cedar rust? It is cheaper to cut down the cedars. Cedar eradication is the cheapest form of orchard insurance you can buy. The cost, on the average, is less than the cost of a single spray application."

Stewart (1920) is of the opinion that orchardists of New York should coöperate and by persuasion remove as many as possible of the cedar trees from about their orchards.

Talbert (1925) recommended that cedars be removed from one-half to two miles around commercial orchards in order to successfully control this fungus under Missouri conditions.

McCubbin (1929) advises the removal of red cedars for a minimum of one-half mile from orchards in Pennsylvania. He also recommends the destruction of all native wild apples from nearby orchards, a very important recommendation.

As a result attendant on propaganda favoring red cedar eradication many apple-growing states enacted some form of law whereby eradication of red cedars could be enforced. Two forms of these laws exist: (a) cedar eradication laws and (b) general plant pest laws. States having these laws are listed below and they are graphically shown in fig. 2.

States having a cedar eradication law	States that have a general plant pest law under which cedar eradication has been enforced
Arkansas	
Kansas	Delaware
Nebraska	Illinois
New York	Minnesota
Virginia	Pennsylvania
West Virginia	Wisconsin

In order to satisfactorily protect apple trees an area of at least one mile in radius around commercial orchards must be free from red cedars. To clear such an area it is usually necessary to remove cedar trees from the land of property owners other than that of the orchardist. This is where the main difficulty arose. Property owners within this area often strenuously objected to their cedar trees being removed to protect neighboring orchards. So numerous and so strenuous have been the objections that in many states the cedar eradication laws are no longer enforced. In Nebraska a case was taken to the Federal District Court of Omaha and aroused so much ill-feeling that it seemed

unwise to continue the enforcement of the law in that state. Quoting from a letter received recently from New York, "There is a cedar eradication law on the books in this state, but at the present time very little effort is being made to enforce it since the chief problem is in the Hudson Valley where large estates are involved and law suits are sure to follow any attempt to eradicate the cedars." One from Illinois reads, "The state attempted to enforce eradication in a limited area but with indifferent success. In some of the states, however, as Kansas and West Virginia, I am told that cedar eradication is being carried out with very good results but often under great opposition.

FIGURE 2. Location of states in which cedar eradication laws (indicated by lines sloping northeastward) or general plant pest laws (indicated by lines sloping northwestward) have been enforced as a means of controlling *G. Juniperi-virginianae*.

(b) Fungicidal control on apples and on red cedars.

In 1888 Col. A. W. Pearson in New Jersey sprayed two apple trees, one with sulfate of iron, and one with Bordeaux mixture. The sprays were applied every three weeks until July 22. Of the first tree he remarked, "At the close of the experiment the trees were as badly affected as at any previous year." Of the second tree Professor B. T. Galloway said, "The foliage remained fairly healthy, yet the benefit resulting was not sufficient return for the labor expended." So far as I have learned this is the earliest recorded attempt to control *G. Juniperi-virginianae*. It was reported in Professor B. T. Galloway's Annual Report of the U. S. D. A. of 1889, and also in a paper by Professor Galloway in 1890.

Jones (1891) sprayed apple trees with ammoniacal copper carbonate on May 17 and 30. The results showed no marked difference in the percent of rusted leaves, but the number of rust spots per leaf was somewhat reduced.

Pammel (1891) reported that he sprayed apple trees with Bordeaux mixture and ammoniacal copper carbonate. Bordeaux was applied twice and the third application was of ammoniacal copper carbonate. He says, "The spraying had apparently no effect on the fungus; it was about as severe on the sprayed trees as on the check."

Emerson (1905) sprayed several apple trees with 4:4:50 Bordeaux and obtained very good control. He stressed that it was essential to spray at the time when the telia were gelatinized and that spraying at other times was useless.

Hein (1908) reported the results of three years of spraying apple trees with Bordeaux mixture. "During the present season, cedars were carefully watched. After each gelatinous state of the cedar apples, the apple trees under experimentation were thoroughly sprayed. This spraying was done as soon as the rain, which caused the swelling of the cedar apples, ceased. The most we can say in favor of the spraying is that the amount of rust may have been very slightly reduced."

Waite (1910) used many spray materials in experiments on the control of cedar-apple rust and other foliage diseases of the apple. He summarized the results by stating that "all the fungicides protected the trees almost completely from fungous diseases."

Bartholomew (1912) obtained fairly good control by spraying apple trees with Bordeaux 4:4:50 and 3:3:50 immediately following the gelatinization of the telia. He insisted that, "The crucial time for action depends entirely upon such weather conditions as favor development of the cedar galls." In this work he sprayed three orchards: one, close to cedar trees; a second, one-quarter mile from cedar trees; and a third, one mile from cedar trees. He tabulated the number of sprayed and unsprayed leaves affected in each orchard and showed a marked reduction in the number of infection spots by spraying.

Giddings and Neal (1912) in a preliminary report stated that they found Bordeaux mixture, lime sulfur and atomic sulfur valuable in the control of *G. Juniperi-virginianae*. The quantity and the quality of the fruits of certain varieties was much higher on sprayed than on unsprayed trees. They found, too, that the time of application was of much importance in spray control work. It was, however, possible to control the disease to some extent by a single application.

Giddings and Berg (1915) stated that "our work thus far has shown that apple rust may be controlled by spraying." They found lime sulfur 1:40 and Bordeaux to be about equal in value and much better than atomic sulfur. They add, however, that it seemed impracticable to control this disease in commercial orchards by use of liquid sprays. They state further that the spraying must, of course, be thoroughly done, and "the impracticability of carrying out such a spray schedule (as six to seven applications) in a large orchard is self-evident."

Reed, Cooley and Crabill (1914) and Reed and Crabill (1915) experimented with several fungicides on the control of cedar rust of apples. They stated that "copper lime sulfur was by all odds the best fungicide employed in this experiment. It gave practically clean foliage and produced no spray injury either to foliage or fruit."

Fromme and Thomas (1917) applied a "superfine" sulfur dust to apple trees in an attempt to control *G. Juniperi-virginianae*, but were entirely unsuccessful in these experiments.

Heald, in 1909, reported the first attempt to control *G. Juniperi-virginianae* by spraying red cedars. "It is obvious that the spraying might be designed to kill the teliospores, and so should be made to prevent the reinfection of the cedar. Germination tests made from the teliospores of the telia sprayed with 5:5:50 Bordeaux showed the complete failure of the teliospores to produce sporidia. It does not seem, however, that spraying at this period will ever be practical. Some carefully planned spraying experiments to prevent the reinfection of the cedar were carried out during the season of 1907. The results showed that spraying at intervals from the period of maturity of the aecia to September 1 very greatly reduced the number of cedar apples. The reduction of number of galls is not sufficient to be of much value in preventing the infection of adjacent apple trees, but if the life of valuable cedars is being threatened, spraying should reduce the ravages of the fungus sufficiently to prevent any material injury to the cedars."

2. My studies and observations on control measures.

My studies in this connection were based almost exclusively on fungicidal means of control. The problem included an exploratory investigation of numerous fungicides with respect to their control value on both apple trees and red cedars. The most promising of these fungicides was then tested on an extensive experimental scale on numerous trees under various weather conditions. The fungicide was applied to

red cedars (a) to prevent germination of the teliospores, (b) to protect cedars from infection by aeciospores, and (c) to apple trees as a protection against basidiospore infection.

(a) On red cedars to prevent germination of teliospores.

On the Lyman estate, Canton, Massachusetts, *G. Juniperi-virginianae* was in very great abundance and exploratory tests with several fungicides were made there. In table IX are enumerated the sprays that were used in these tests.

TABLE IX.

SPRAY AND DUST MATERIALS USED IN EXPLORATORY TESTS

Bordeaux	3:3:50, 4:4:50, 6:6:50
Linco colloidal sulfur[1]	¼%, ½%, 1%, 2%, 3%
Lime-sulfur	1:30, 1:40, 1:50, 1:70
Soluble palustrex[2]	1%, 2%, 3%, 4%
" " A.	" " " "
" " B.	" " " "
" " C.	" " " "
Sunoco oil[3]	2%, 4%
50% Sunoco oil and 50% soluble palustrex	2%, 4%
50% Sunoco oil and 50% soluble palustrex B.	2%, 4%
80% Sunoco oil and 20% copper resinate	2%, 4%
80% Sunoco oil and 20% soluble palustrex	2%, 4%
Kolo base	
Kolo dust	
Pomo green	
Sulfur dust	

[1]Obtained from Linder and Co., 296 North Beacon St., Boston, Mass.
[2]Obtained from E. W. Coolidge, Jacksonville, Florida.
[3]Obtained from Sun Oil Co., Boston, Mass.

All of these spray and dust materials were first applied to potted red cedars in the greenhouse in the spring. None of them caused burning of the young foliage. In the field the sprays were applied to the galls as follows: (1) before the telia had emerged from the galls, (2) just after the telia had emerged, and (3) after one, two or three gelatinizations of the telia, but always when the telia were dry.

Telia to which the sprays were applied were brought into the laboratory for examination; smear slides were made of the spores and exam-

ination was completed shortly after their arrival. It was not the purpose of this examination to determine the relative value of each spray, rather the purpose was to determine which ones would prevent germination of the teliospores. The most satisfactory sprays were soluble palustrex B at 4% and Linco colloidal sulfur at 1%, 2% and 3%. In testing these sprays further it was found that this colloidal sulfur at 2% and 3% was most constant in its reactions. Colloidal sulfur was, therefore, chosen for the experimental work that followed. It should be added, however, that colloidal sulfur at 1% greatly reduced the amount of germination; colloidal sulfur at 2% completely prevented germination of the teliospores of *G. Juniperi-virginianae*. Colloidal sulfur at 3%, therefore, was unnecessary.

In April 1933, many telia of *G. Juniperi-virginianae* were sprayed upon their first appearance with colloidal sulfur at 1% and 2%. The effect of the spray was determined by gathering several sprayed and unsprayed telia three days after they were sprayed, thoroughly wetting and keeping them in a moist chamber over night. When germination was abundant a spore print would result, but when no spore print was formed a smear slide was made and the teliospores examined under the microscope. The unsprayed teliospores always germinated in abundance. Teliospores sprayed with 1% colloidal sulfur germinated to some extent, but few basidiospores germinated. Telia sprayed with 2% colloidal sulfur showed no germination of the teliospores.

After the rain following each spraying, telia were again gathered and immediately tested. The controls germinated in abundance. The telia sprayed with colloidal sulfur at 1% and 2% germinated to a slight extent. Some change was called for in order to control this small amount of germination. Certain substances were used to lower the surface tension of the spray material which might aid its penetration into the telium. Spreaders were tried but with no success.

Microscopic sections were cut from dry and wet telia and examined in a minimum of water. The structures of the telium gave a clue to a new line of experiment. The telia, it will be recalled, are made up of an outer zone which contains most of the teliospores and an inner and larger zone which contains teliospore stalks largely. To be of most value, therefore, the particles of spray materials should be located on the outside of the telium on or near the teliospores. The next step, therefore, was to find a sticker and spreader so that the sulfur particles might be held on the teliospores or within the spore containing zone. Calcium casienate was the only one used. Again a

new lot of telia were sprayed with colloidal sulfur 2% plus ¼% calcium casienate. Telia were tested in the laboratory and gave positive results for the controls and negative results for those sprayed. Following a heavy rain control as well as sprayed telia were examined for germination. All unsprayed telia germinated in great abundance. Examination of the sprayed telia of *G. Juniperi-virginianae* showed that teliospores in the sprayed portion of the telium did not germinate but that an additional basal portion of the telium which had not been touched by the spray had emerged from the gall, and the teliospores in this portion germinated in abundance. Following another heavy rain sprayed and unsprayed telia of *G. Juniperi-virginianae* were collected for immediate examination. The controls germinated in great abundance. The sprayed portions of the telia showed, after these two rains, no germination of the teliospores. An additional part of the base of each telium had emerged in this rain. The teliospores in this new portion of the telium germinated in great abundance. Photographs of telia which were sprayed and later subjected to rains are shown in plate 96, figs. 5 and 6. From these observations and data it was concluded that in order to successfully control these rusts by spraying on the red cedar it was necessary to spray the telia after each rain with colloidal sulfur 2% plus ¼% calcium casienate.

(b) On red cedars as a protection against infection by aeciospores.

Investigations on this means of controlling *G. Juniperi-virginianae* are now in progress. However, no experimental data are yet available with respect to the value of spray applications on red cedars.

(c) On ornamental apples as a protection against infection by basidiospores.

In the summer of 1932 certain of the most susceptible species of *Malus* were sprayed in an effort to determine the relative values of soluble palustrex B and colloidal sulfur. Branches of *M. coronaria Charlottae* and *M. Soulardi* were sprayed with soluble palustrex B at 1% and 2%, and other branches were sprayed with colloidal sulfur ¼% and ½%. The next day, all of the sprayed branches and four control branches on each tree were heavily inoculated with basidiospores of *G. Juniperi-virginianae* by the usual method. The results are given in table X.

From these data it was concluded that colloidal sulfur at ½% was the most efficient spray material with which to protect aecial hosts.

Since sulfur and sulfur compounds have proven to be effective generally in controlling rusts, it was decided to concentrate on the use of colloidal sulfur during the next season.

TABLE X.

RESULTS OF SPRAY EXPERIMENTS WITH COLLOIDAL SULFUR AND SOLUBLE PALUSTREX B

	col.sulfur ⅛%		col.sul.¼%		sol.pal.B 2%		sol.pal.B 1%	
Test trees	no. lvs. inoc.	no. infection spots	no. lvs. inoc.	no. inf. spots	no. lvs. inoc.	no. inf. spots	no. lvs. inoc.	no. inf. spots
Malus Soulardi	21	4	22	8	26	16	25	6
coronaria Charlottae	21	2	26	50	28	50	20	100
Totals	42	6	48	58	54	66	45	106
Controls	All leaves heavily infected							

In the spring of 1933 extensive control experiments were conducted on certain of the most susceptible species of the genus *Malus*. Convenient portions of the trees were sprayed with colloidal sulfur ½% and the remaining portion served as controls. A total of 250 inoculations were made on the sprayed and unsprayed branches. The results of these tests showed conclusively that colloidal sulfur at ½% gave excellent protection to the leaves of the most susceptible apple trees. A typical example of the results is shown in plate 91, figs. 4 and 5. The twig in fig. 5 was unsprayed, while the twig in fig. 6, was sprayed; both were inoculated at the same time and under the same conditions. It will be observed that many lesions developed on the unsprayed leaves while no infection developed on the sprayed ones. Spray experiments were repeated many times during the summer and the results were consistent. Data on these experiments are presented in table XI. These data indicate that under experimental conditions colloidal sulfur has been entirely satisfactory in controlling *G. Juniperi-virginianae* on apple trees. Much encouragement is offered in regard to the employment of this spray material on a practical scale in apple orchards. It is my conviction that spray problems arising in practical control work can be overcome. The cost of colloidal sulfur does not exceed that of good spray products. Its control value and adhesiveness have been shown to leave little that is desired and it seems not to be injurious to either the leaves or fruit.

The following data also favor further investigations of colloidal sulfur as a practical orchard spray material. It has been shown by other workers that the spores of the apple scab organism, *Venturia inaequalis* (Cke.) Wint., are distributed during early spring rains. The distribution of these spores usually coincides with that of basidiospores of *G. Juniperi-virginianae*. It has also been shown that sulfur-containing fungicides will control apple scab. Therefore, it seems highly desirable that joint control of these two organisms by means of colloidal sulfur be thoroughly investigated. A program for this purpose is now in progress.

X. RECOMMENDATIONS

With the advantage of additional information now at hand it seems that both apple trees and red cedars may be grown in close proximity and at the same time practically free from *Gymnosporangium* rusts. Certain precautions, however, will greatly aid in the furtherance of such a scheme. The aecial hosts of the cedar-apple rust fungus are now known to be all of the North American species of the genus *Malus* and *M. sylvestris* of Europe. *Malus baccata* and *M. floribunda* have also been reported as susceptible. For practical purposes, those hosts on which spermogonia were developed (and these in small numbers) may be considered as immune since they cannot reproduce the rust. We have, therefore, a wide range of rust-free species and varieties from which to choose. Many of these vie with native apples in their beauty and adaptability as ornamental trees. Most of these have brightly colored fruits also, in contrast to the plain green of native species. All of the foreign species and varieties given in this study are hardy in the Arnold Arboretum. So far as I am aware no serious disease is liable to cause especial trouble to them. If orchard apples are desired in regions where red cedars are common, helpful information regarding the relative susceptibility of some 300 varieties will appear shortly in another publication. The *Juniperus* hosts of the cedar-apple rust fungus are the native *J. virginiana, J. horizontalis* and *J. scopulorum* and several varieties of each (see page 175). All other native species and all of the foreign ones have thus far proved to be immune. Several of the immune species and varieties bear a close resemblance to our native susceptible ones and these may be employed with satisfactory results. If, however, susceptible apples and red cedars are desired on adjacent plots, each may be effectively protected from the contagion by a screen of taller non-susceptible trees.

While planting programs are very effective in controlling this rust, eradication measures even on a limited scale may also prove very effec-

tive. Wild or scrubby apple trees as well as red cedars may be the source of inoculum infecting more prized specimens. As a control measure it is very desirable that such weed trees be removed. Cases have been known where a single scrub apple tree was for many seasons the source of inoculum causing a great deal of damage to a large grove of ornamental cedars.

Pruning out galls from cedar trees is generally not effective. Too many, especially of the smaller ones, are likely to be missed; moreover, to be effective they would have to be removed throughout a very wide area. Of course, under exceptional conditions removal of galls

TABLE XI.

RESULTS OF SPRAY EXPERIMENTS WITH LINCO COLLOIDAL SULFUR ½% PLUS CALCIUM CASIENATE ¼% DURING THE SUMMER OF 1933, ON M. IOENSIS PLENA

Date of inoculation	Experiment no.	Results on sprayed branches	Experiment no.	Results on unsprayed branches	Remarks
June 12	1	*0	3	*3	Spray applied
	2	0	4	3	June 10.
13	5	0	7	3	Heavy rain
	6	2	8	3	June 12, P. M.
14	11	0	9	3	
	12	0	10	3	
15	13	0	15	2	
	14	0	16	3	
16	17	0	19	3	Showers
	18	0	20	3	
17	21	0	23	3	Showers
	22	0	24	2	
18	25	1	27	3	Rain; A. M.
	26	2	28	3	
19	33	3	35	2	
	34	2	36	3	
20	--	-	--	-	
21	53	3	49	3	
	54	died	50	3	
22	57	1	61	3	
	58	2	62	3	
23	65	2	67	3	
	66	3	68	2	
24	--	-	--	-	
25	84	0	81	3	Spray applied
	84	0	82	3	on another tree
26	87	0	85	3	June 25.
	88	0	86	3	
27	93	1	95	3	
	94	0	96	3	
28	100	0	102	1	
	101	1	103	2	
29	109	0	111	2	Rain
	110	0	112	2	
30	113	0	115	2	
	114	0	116	3	

July 1.	125	0	127	1	
	126	lost	128	lost	
2	133	1	135	3	Rain
	134	0	136	3	
3	143	0	145	3	
	144	0	146	3	
4	155	1	153	3	Rain
	156	2	154	3	
5	---	-	---	-	Heavy rain
6	163	2	165	3	
	164	2	166	3	
7	173	3	175	3	
	174	3	176	3	
8	183	3	185	3	
	184	1	186	3	
9	195	0	197	3	Spray applied
	196	0	198	3	on another tree
10	201	0	203	3	July 9, A. M.
	202	0	204	3	Showers July 9,
11	207	0	209	3	P. M.
	208	0	210	3	Rain July 10.
12	213	0	215	3	
	214	1	216	3	
13	220	0	218	3	
	221	0	219	3	
14	225	0	227	3	
	226	1	228	3	
9	193	0	Controls as in the foregoing for July 9-14.		Spray applied to another portion of tree; No cal. cas. used. Remarks as in the foregoing for July 9-14
	194	0			
10	199	0			
	200	0			
11	205	0			
	206	0			
12	215	0			
	216	0			
13	221	0			
	222	0			
14	223	0			
	224	0			

*Refers to the amount of infection as follows:

0 — none
1 — slight
2 — moderate
3 — heavy

may be practicable. If in small isolated groups of cedars a few scattered galls have developed, every one of these could be removed before the buds of susceptible apple trees have begun to open, and good protection would result.

Fungicidal control of the rust on apple trees now gives promise of practicability. It has proved successful in my experimentation under controlled inoculation by using Linco colloidal sulfur at ½% strength. Tests under natural conditions are warranted. The time of application of the fungicide is very important and should coincide with the times of discharge of the basidiospores while the leaves are within their period

of susceptibility. The following spray schedule should be closely followed for the protection of orchard apples:

First application—Before the first expected rains after the leaf buds have opened. This will be about the first of May in Massachusetts and under certain conditions may coincide with the second application.

Second application—After the cluster buds have separated but before the petals have expanded. This is the "pink spray" of the apple scab schedule.

Third application—When the petals are about two-thirds off. This is the "calyx spray" of the apple scab schedule.

Fourth application—Ten days to two weeks later. Shorter intervals may be necessary if the weather is rainy. Colloidal sulfur will remain effective after two heavy or three moderate rains.

Fifth application—Need only be applied if the telia are still present on cedar trees and should occur ten days to two weeks later than the fourth application.

The foregoing spray schedule is based on stages of development of the flowers and applies particularly to orchard apples. The native ornamental apples, however, develop their foliage to a much greater extent than do orchard apples before flowers appear on the former. Thus certain modifications of the schedule are called for. The directions for the first application will apply to all trees. On the native ornamental apples the second application should be given from four to seven days after the first application. The third application seven to ten days after the second and the fourth and fifth applications in ten days to two week intervals. Variations in this schedule will be due to growing conditions and to rains. It must be borne in mind that the leaves should be well covered with the fungicide before rains. Linco colloidal sulfur will adhere and remain effective through about two heavy rains or three moderate ones. Thus, more frequent applications will be required if rains are abundant. The spray schedules as outlined above coincide with that generally recommended for the control of apple scab and this organism will be simultaneously controlled by the use of Linco colloidal sulfur. To control feeding insects, four pounds of arsenate of lead should be added to each one hundred gallons of the spray mixture.

Fungicidal control measures for application to red cedar cannot as yet be outlined with the same explicitness. The reason for this lies in the circumstance that it remains yet to be determined just when infection takes place. Since infection results from the spores discharged from the lesions on apple trees and some of them, though the percentage is very small, are immediately viable, it follows that protection should be afforded red cedars when their discharge begins. In Massachusetts this is about the first of July. The red cedars should, therefore, have a protective spray cover throughout July. It is possible that spores discharged later in the season may also cause infection. In such a case the spraying would have to be repeated in August and possibly September. My own tests are not sufficiently advanced to give the desired answer. A colloidal sulfur, such as Linco (½% strength) is advised.

XI. SUMMARY

1. Inoculations and examinations for infection were made on 108 species of 11 genera of plants in the Arnold Arboretum with *Gymnosporangium Juniperi-virginianae* from Massachusetts. The genera were *Amelanchier, Comptonia, Crataegomespilus, Cydonia, Malus, Myrica, Photinia, Pyrus, Sorbaronia, Sorbopyrus* and *Sorbus*. In addition field observations were made on 942 species of *Crataegus*.

2. The results of the inoculation experiments show that:

(a) All of the species and varieties (16 in number) of the section Chloromeles of the genus *Malus* and two other species, namely, *M. fusca* and *M. sylvestris*, produced aecia. The hosts showed differences in their degree of susceptibility to the fungus.

(b) Twelve species and varieties found in other sections of the genus produced spermogonia only. The infection spots were always few and the spermogonia were very irregular both in their time and in their manner of development.

(c) Other species and varieties of *Malus* (47 in number) and all other species tested or observed were found to be immune.

(d) The hosts on which aecia were produced were found to be susceptible for various periods of time. The most susceptible hosts could be infected throughout the greater part of the growing season. The less susceptible ones could be infected for progressively shorter periods down to about two weeks.

3. Examination of the genus *Juniperus* in the Arnold Arboretum showed that *J. virginiana* and twelve of its varieties, *J. scopulorum* and

two of its varieties, *J. horizontalis* and two of its varieties were susceptible to *G. Juniperi-virginianae*. Fifty-two species and varieties were immune.

4. The morphological and histological symptomatology of the disease on *Malus* spp. showed that the disease was most severe on the more susceptible hosts and less severe on the more resistant ones. The forced growth of infected buds, a phenomenon which seems to be confined to species and varieties of wild apples, is herein described for the first time. The geographical distribution of the pomaceous hosts, with one exception (*M. sylvestris* of Europe), and of the *Juniperus* hosts was confined to North America. The disease was found throughout the coinciding ranges of the hosts in the section Chloromeles and *J. virginiana* in eastern North America. The disease was not found within the range of *J. scopulorum* or *M. fusca* in western North America.

5. The life history of the aecial phase of the organism showed marked differences in the development of the mycelium and the fructifications on hosts of various degrees of susceptibility. The fungus developed most luxuriantly on the most susceptible hosts and less so on the more resistant ones.

6. To the life history of the telial phase little has been added; however, it was shown that a zone of fresh teliospores is produced by the telium after each of six or seven consecutive rains in the spring.

7. The possibility of biological strains of the fungus was investigated by employing telial material from eight states, namely, Alabama, Kentucky, Massachusetts, Michigan, Missouri, Nebraska, New York and West Virginia. The results showed that biological strains of this rust were present.

8. Several factors are discussed with respect to their influences on susceptibility, resistance, immunity and control on apple trees as well as red cedars.

9. Eleven states in eastern North America reported that they have either a cedar eradication law or a general plant pest law under the protection of which attempts have been made to eradicate red cedars from around productive orchards as a means of controlling the cedar-apple rust. Most of these states no longer enforce cedar eradication.

10. Several fungicides have been examined with respect to their value in controlling *G. Juniperi-virginianae*. Of these, a form of colloidal sulfur has given especially promising results in experimental tests to control the fungus on apple trees.

11. Recommendations have been discussed with respect to control measures by means of (1) selective plantings, (2) eradication of wild or scrubby apple and red cedar trees and (3) fungicides applied to apple trees in the spring and to red cedars in the summer and fall.

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EXPLANATION OF PLATES

Plate 91

Fig. 1. Spermogonia of *Gymnosporangium Juniperi-virginianae* on a mature leaf of *Malus glabrata,* a moderately susceptible species. The spermogonia, though numerous, are in small groups.

Fig. 2. Spermogonia on a young leaf of *M. Soulardi,* a very susceptible species. Large groups of spermogonia are characteristic of very susceptible species of *Malus.*

Fig. 3. Spermogonia along the midrib of *M. coronaria Charlottae.* The infection spots are fully mature and the yellowish-red peripheral zone is clearly marked.

Fig. 4. Fully mature infection spots on the very susceptible *M. ioensis plena,* showing their large size and the yellowish-red peripheral zone.

Fig. 5. Numerous infection spots on fully mature leaves of *M. ioensis plena.* Note that on the youngest leaves infection spots are larger and more numerous than the older leaves. This is a photograph of an unsprayed control branch inoculated July 20, 1933. Compare with figure 6.

Fig. 6. Branch of *M. ioensis plena* sprayed with Linco colloidal sulfur ½% plus calcium casienate ¼% and inoculated at the same time and under the same conditions as the branch in figure 5. Note that on this branch no infection spots were produced.

Fig. 7. Enlarged view of spermogonia on a leaf of an orchard apple. (After Giddings and Berg 1918.)

Plate 92

Fig. 1. Developing spermogonium on *M. ioensis plena* 8 days after inoculating. The buffer cells are rapidly expanding and push- the epidermis upward.

Fig. 2. Developing spermogonium on the same leaf as fig. 1. The buffer cells are almost completely disintegrated and the spermatiophores are beginning to constrict spermatia. Figs. 1 and 2 ×400.

Fig. 3. Fully mature spermogonia on the leaf of *M. platycarpa.* ×70.

Fig. 4. Microscopic section of the whole infected area of *M. prunifolia.* ×70. The abortive spermogonium and limited infection area are typical of those host species on which only spermogonia develop.

Fig. 5. Diagram to show the location of measurements for spermogonia. h = height; w = width; d = depth to which the spermogonium is sunken beneath the epidermis.

Plate 93

Fig. 1. Infection cushions on a leaf of the very susceptible *M. coronaria Charlottae.* Large aecial cushions are typical of very susceptible hosts. Collected September 6, 1933. Nat. size.

Fig. 2. Infection cushions on a leaf of the moderately susceptible *M. platycarpa.* Aecial cushions of this size are typical of moderately susceptible hosts. Collected September 6, 1933. Nat. size.

Fig. 3. Infection spots on a leaf of the very resistant *M. fusca.* Collected September 6, 1933. On this date only one infection spot near the tip of the leaf remained alive, all others had died, and

with them a portion of the leaf tissues. Small aecial cushions and dead infection spots after September 1 are characteristic of resistant species. Nat. size.

Fig. 4. Enlargement of an aecial cushion on a leaf of *M. ioensis plena.* The concentric arrangement of the aecia is characteristic of very susceptible species. ×10.

Fig. 5. Enlargement of aecia on the fruit of an orchard apple. On fruits, aecia have no regular arrangement. ×10.

Fig. 6. Aecia on the calyx end of a fruit of *M. Soulardi.* Nat. size.

Fig. 7. Aecia on the pedicel of a fruit of *M. ioensis plena.* Nat. size.

Fig. 8. Aecia on one side of a fruit of *M. ioensis plena.* Nat. size.

Fig. 9. Aecia all over a fruit of *M. ioensis plena.* Nat. size.

Plate 94

Fig. 1. Photomicrograph at the border of an infection cushion on a leaf of *M. ioensis plena.* ×20. This shows clearly that the mesophyll is very greatly enlarged while the palisade tissue is quite unchanged morphologically. Compare the hypertrophy on this native species with that of a foreign species shown in plate 92, fig. 4. They are of about the same age. The latter figure is ×70 while this one is ×20.

Fig. 2. Young aecium on a leaf of *M. platycarpa.* A large number of apical peridial cells are present, but only a few aeciospores have been formed.

Fig. 3. Aecium of *G. Juniperi-virginianae* from *M. platycarpa* at a somewhat more mature stage. Numerous aeciospores and lateral peridial cells have developed.

Fig. 4. Diagrammatic drawing of spermogonia and aecia in several developmental stages. After Reed and Crabill (1915).

Fig. 5. Outline drawings of several aeciospores of *G. Juniperi-virginianae.*

Fig. 6. Drawings of peridial cells of *G. Juniperi-virginianae.*

Fig. 7. Haustoria of *G. Juniperi-virginianae* in the leaf and fruit tissues.

Plate 95

Fig. 1. Forced growth of an infected bud of *M. Soulardi,* harvested September 3, 1932. Mature aecia are present on the base of the bud and spermogonia on the petiole of the outermost leaf.

Fig. 2. Forced growth of an infected bud of *M. bracteata,* harvested September 15, 1932. Spermogonia are present on blades of the youngest leaves, and aecia are in progressive stages of development on the midribs of the older leaves.

Fig. 3. Forced growth of an infected bud of *M. ioensis plena.* Spermogonia are present over all of the upper surfaces of the misshapen leaves. Note the forced growth of a lateral bud at the base of the infected tissues of the twig.

Fig. 4. Shows aecia scattered irregularly over the lower surface of a leaf on the same twig as in fig. 3.

Fig. 5. A row of nursery plants of *M. ioensis plena* every twig of which was attacked and the plants were killed outright. It will be noted that the killed plants are between rows of a foreign species, *M. floribunda* which are in excellent health. Next to these on the right is a row of red cedars infected with *G. Juniperi-virginianae.*

Fig. 6. Forced growth of a lateral bud of *M. bracteata*. Compare with the normal bud near the base of the infected tissues.
Fig. 7. Winter aspect of a forced grown bud of *M. angustifolia*. The leaves of forced buds usually remain attached all winter and the portion of the twig beyond the bud is usually killed.

Plate 96

Fig. 1. A red cedar tree heavily infected with *G. Juniperi-virginianae*.
Fig. 2. A branch from the tree in figure 1 showing galls of various sizes.
Fig. 3. Average-sized galls as seen in early March.
Fig. 4. First appearance of telia of *G. Juniperi-virginianae* after a rain in late March or early April.
Fig. 5. Telia as seen after an additional rain.
Fig. 6. Telia as seen after two rains.
Fig. 7. Telia fully expanded. These are typical of the rust during spring rains.
Fig. 8. Telia at the end of the season of sporulation.

Plate 97

Fig. 1. Galls of *G. Juniperi-virginianae* in winter condition on red cedars of very poor health. Note the convoluted, shrunken appearance of the galls.
Fig. 2. A gall that produced one crop of telia and continued growth from its base for another season.
Fig. 3. Stages in the development of galls on red cedars.
Fig. 4. Galls on subulate leaves of red cedars.
Fig. 5. These telia were sprayed shortly before a rain. Note that the sprayed portion of the telia gelatinized but slightly; the more expanded portion emerged during the rain.
Fig. 6. These telia were also sprayed shortly before a rain. Note that the tip gelatinized to a very limited extent, the more robust basal portions were added during two subsequent rains. A constriction in the swollen basal part of each telium lies between the additions made during the rains.
Fig. 7. A spore print of basidiospores of *G. Juniperi-virginianae*.

Plate 98

Fig. 1. Photomicrograph of a cross section of two depressions in a gall of *G. Juniperi-virginianae*. Early stages of the development of the telium are shown.
Fig. 2. Stages in the development of teliospores of *G. Juniperi-virginianae*.
Fig. 3. Outline drawings of teliospores of *G. Juniperi-virginianae*.
Fig. 4. Cross section of the telium of *G. Juniperi-virginianae*. It will be seen that teliospores are located chiefly on the periphery of the telium.
Fig. 5. Camera lucida drawings of haustoria of the telial phase in cells of the galls of *G. Juniperi-virginianae*.

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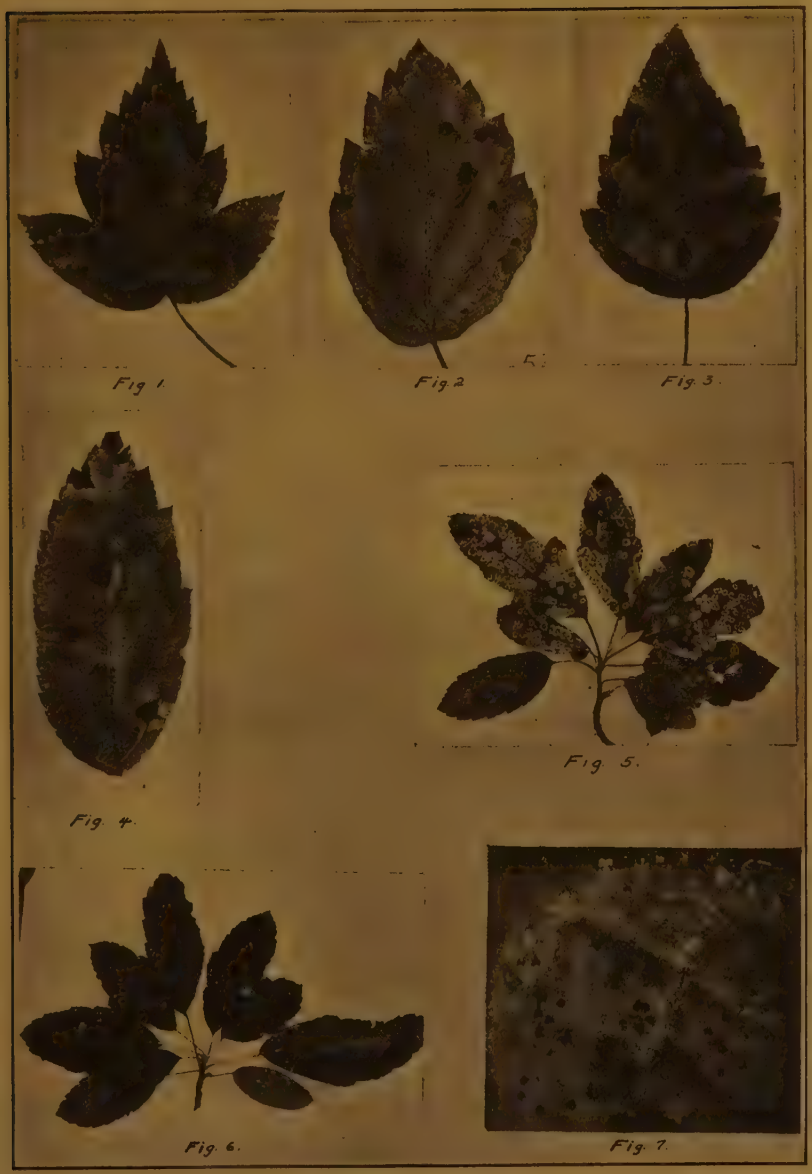

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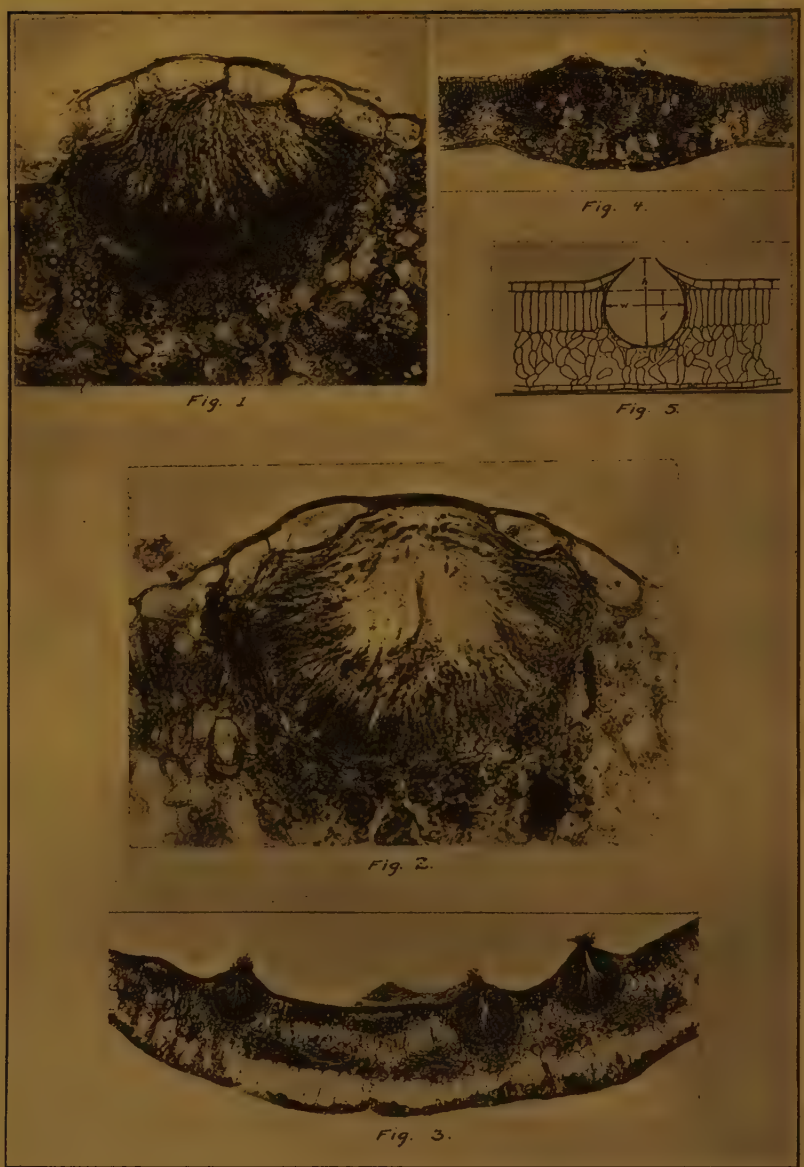

Fig. 1

Fig. 4.

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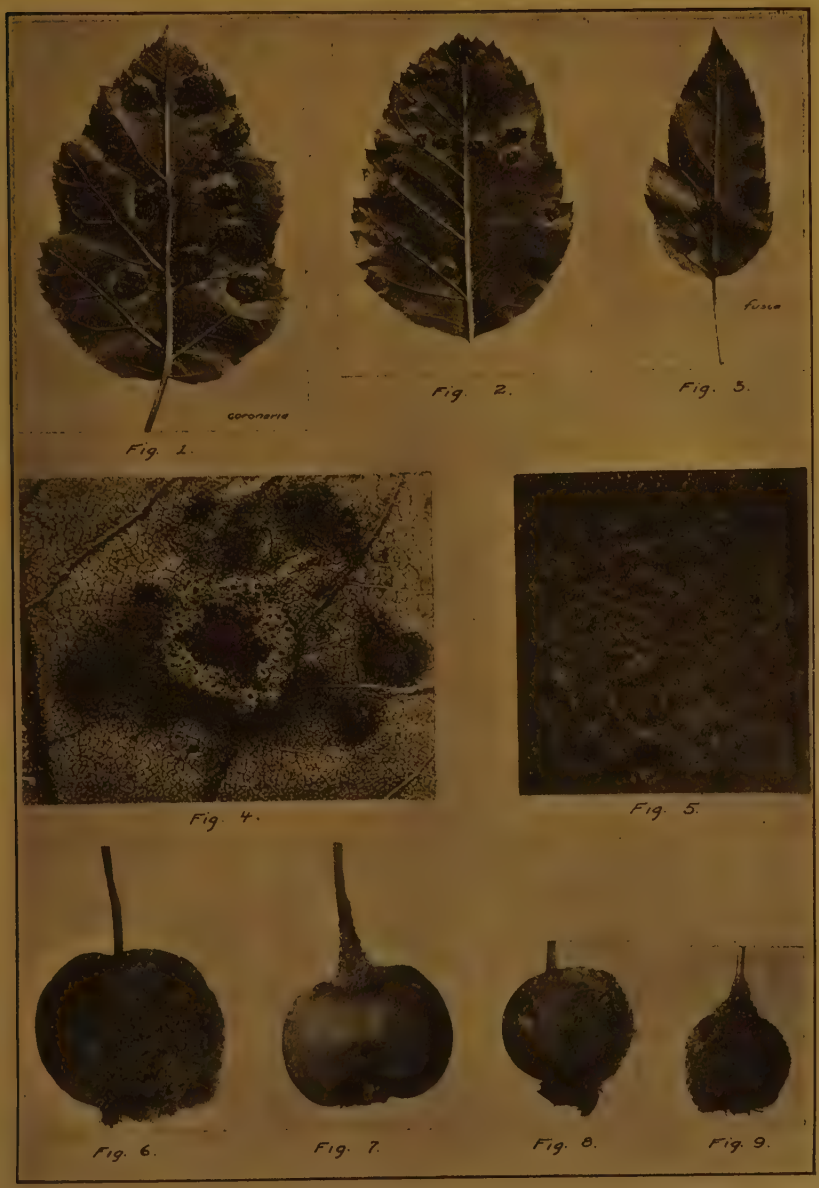
Cedar-Apple Rust Fungus



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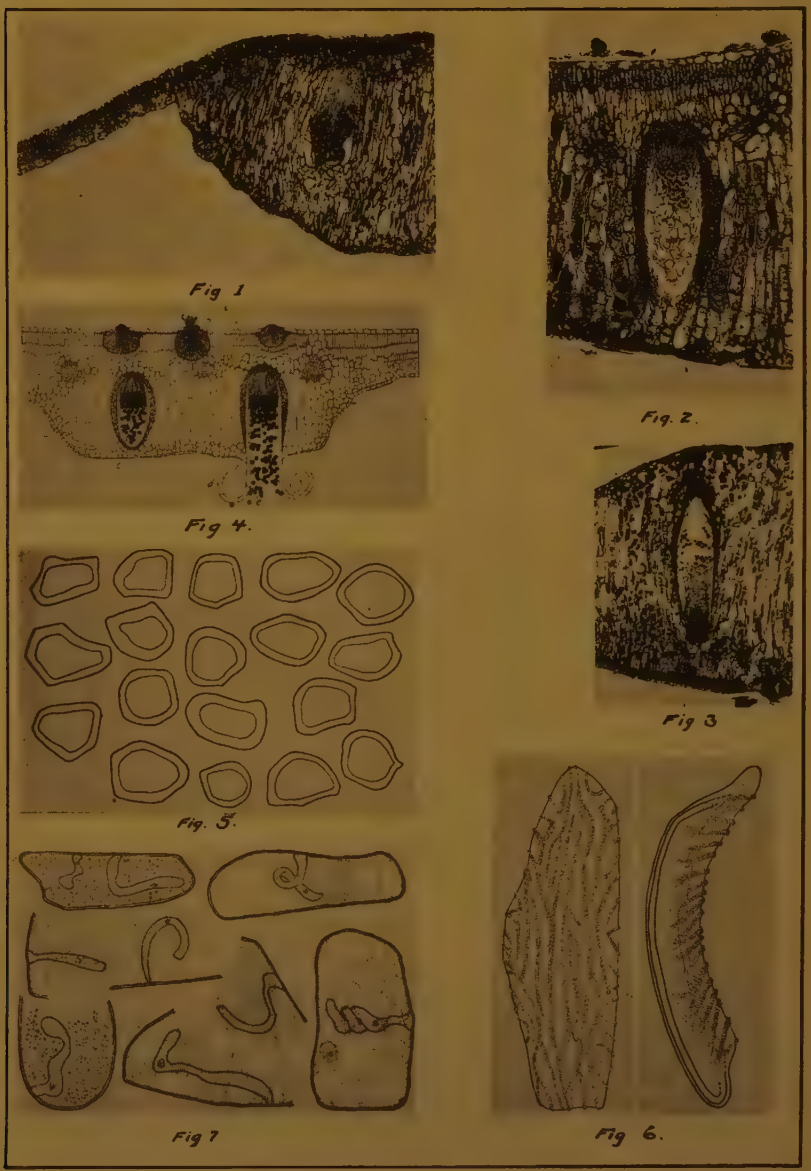

CEDAR-APPLE RUST FUNGUS

Cedar-Apple Rust Fungus

Cedar-Apple Rust Fungus

Cedar-Apple Rust Fungus

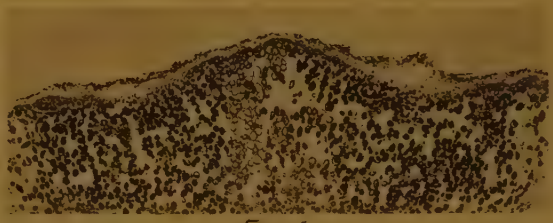

Fig 1

Fig. 2

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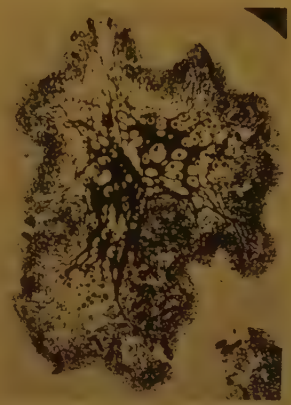


Fig. 4.

Fig. 5.

CEDAR-APPLE RUST FUNGUS

THE CAMBIUM AND ITS DERIVATIVE TISSUES

NO. IX. STRUCTURAL VARIABILITY IN THE REDWOOD, SEQUOIA SEMPERVIRENS, AND ITS SIGNIFICANCE IN THE IDENTIFICATION OF FOSSIL WOODS

I. W. Bailey and Anna F. Faull

With one text figure and plates 99-106

INTRODUCTION

Systems of classifying the woods of conifers and dicotyledons have developed largely through trial and error, and in many cases do not provide a reliable basis for the identification of fossilized specimens. This is due to the fact that comparatively little is known concerning the limits of variability of the diagnostic criteria used in the construction of keys.

In the seventh paper of this series (Bailey, 3) it was shown that a number of the so-called transitional Mesozoic Coniferæ fall within the range of variability of living representatives of the Pinaceæ-Abietoideæ. If *Protocedroxylon, Planoxylon, Protopiceoxylon,* etc., are to be classified as Protopinaceæ or Araucariopityeæ, then so should certain specimens of the wood of *Cedrus, Keteleeria,* and other extant genera. Such paradoxical situations can not be fully clarified until large collections of authentic specimens are assembled, not only from different genera, species, and geographical races, but also from different parts of the tree and from trees growing under different environmental conditions.

In choosing a species for an investigation of the range of variability of anatomical characters, it seemed advisable to select the redwood, *Sequoia sempervirens* Endl. This tree is of unusual interest not only because of its large size and longevity, but also because it belongs to a genus which has been, and still is, the subject of frequent discussion in paleobotanical literature.

MATERIAL

Most of the material from mature stems of large diameter was collected by Professor A. E. Douglass in connection with his investigation of tree rings. Entire cross sections were secured from different heights in the tree and from trees growing in different parts of the extensive range of the redwood. Small specimens suitable for anatomical study were removed along specific radii of these huge cross sections. Specimens from roots, branches, and stems, of both seedling-

trees and sprout-trees, were collected by the senior author in Mendocino and Monterey counties. Additional material was obtained through the kind assistance of Mr. Frank Poulter, Professor Emanuel Fritz of the University of California, Mr. H. L. Person of the California Forest Experiment Station, Dr. D. T. MacDougal and Mr. F. W. Haasis of the Carnegie Institution, and others.

GROWTH LAYERS

The growth layers of the redwood, as seen in transverse sections, vary considerably in width, in the ratio of latewood to earlywood, and in the abruptness of the transitions between thin-walled and thick-walled tracheids, *Figs. 1-13.* In young trees growing under favorable environmental conditions, the growth layers of the stem commonly attain a width of from 4-10 millimeters, *Fig. 11.* During the subsequent development of the trees, the rings tend to become narrower and narrower, *Figs. 3-5,* and may actually be reduced at times to the theoretical minimum of two tracheids, i.e., one thin-walled cell and one thick-walled cell, (a) in *Fig. 5.* Such sequences of growth layers of decreasing width, although of not infrequent occurrence, are by no means a characteristic feature of all redwoods. The species grows naturally in forests of the "selection type," and a large proportion of the trees originate as sprouts which develop in deep shade and are forced to grow for a varying period of years in a more or less suppressed condition. Thus, many of the trees in virgin forests have relatively narrow rings throughout the stem, or alternating zones of narrow and wide rings; for even old suppressed trees may form wide rings, *Fig. 13,* when released from the competition of their dominating neighbors (Fritz, 12), or in response to specific tropisms, *Fig. 6.* Excentric arcs of abnormally wide growth layers, false rings, *Fig. 12,* incomplete rings (Fritz and Averell, 11), and burly or curly structures are of very common occurrence. As stated by Fisher (10), "the tree's vitality is so great, it endures so many vicissitudes, and suffers from so many accidents in the centuries of its existence, that the grain of its wood becomes uneven in proportion as its life has been eventful." The growth layers of branches and roots, *Figs. 7-10,* tend to be narrower than those of stems of comparable ages. It is evident, accordingly, that in the redwood as in many other Coniferæ, width of annual ring is a fluctuating character which varies within rather wide limits, not only within different parts of a single tree, but also within homologous portions of trees having different developmental histories.

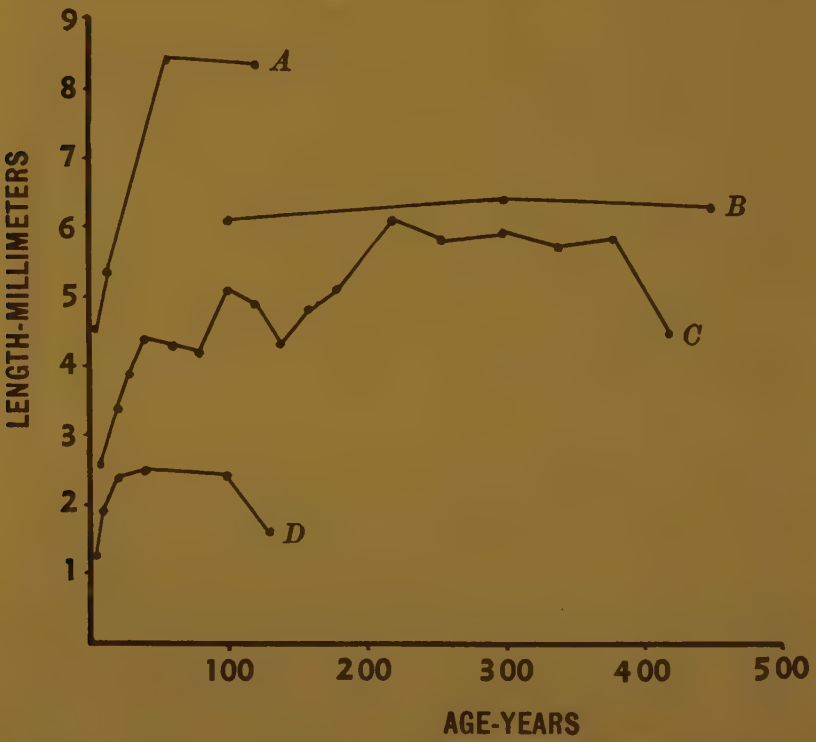
In narrow rings from the peripheral portions of old stems, roots, and branches, *Figs. 4, 5, 8,* and *10,* the ratio of latewood to earlywood is

low, 1:6 to 1:20, and the transitions between thin-walled and thick-walled tracheids are very abrupt; whereas in wide rings, *Figs. 3, 6,* and *13,* the ratio tends to be higher, 1:3 to 4:7, and the transitions may be either gradual, *Fig. 13,* or abrupt, *Figs. 3* and *6*. In the inner rings of stems and branches, the ratio of latewood to earlywood tends to be lower in the wider rings, *Figs. 1, 2, 7, 11,* and *12,* and the transitions between the two types of tracheids to be so gradual that it is difficult to determine with certainty just where the earlywood leaves off and the latewood begins. Paul (23) and Luxford and Markwardt (22) have shown that in the case of second-growth redwood, specific gravity and strength values are lower in open grown trees with large crowns and wide rings than in trees of densely stocked stands with small crowns and narrower rings, the differences being due, in ultimate analysis, to variations in the ratio of latewood to earlywood. It should be emphasized, however, that there are numerous exceptions to these general tendencies, particularly in "compression wood" (Hartig, 16), and in tissues growing under abnormal conditions. For example, *Fig. 9* is a transverse section of "compression wood" from the under side of an old slowly growing branch. The narrow rings are composed entirely of thick-walled tracheids, and it is difficult to distinguish the limits of the individual growth layers.

TRACHEARY ELEMENTS

The size, form, and arrangement of the tracheids—of both earlywood and latewood—vary markedly in different parts of a single tree and in homologous parts of trees which have had different developmental histories. As shown by Sanio (27), Hartig (15), Shepard and Bailey (29), and subsequently by many others, the tracheids of Coniferæ are smaller in the inner than in the outer rings of the stem. This is due primarily to an increase in the length and tangential diameter of the cambial initials, particularly during the earlier years of the meristematic activity of the cambium (Hartig, 15; Bailey 1, 2). Thus, in passing from the pith outward through the xylem of old, straight-grained, symmetrical stems, the derivatives of the cambium become longer and wider until they eventually attain dimensions which remain more or less constant through succeding annual rings. The detailed investigations of Bailey and Tupper (4) indicate that in any particular radius of the stem, the size-on-age curve, or one or more portions of it, may deviate from the normal, owing to the effects of various modifying factors. For example, the distorted tissue formed subsequent to injury, or in response to abnormal conditions of growth, commonly possesses shorter tracheids than normal tissue. Similarly, tissue formed in regions of the tree

where there are mechanical stresses, i.e., at the junction of stems and roots or branches, or in bent or deformed stems, tends to have smaller tracheids than normal, straight-grained tissue. Therefore, the largest tracheids usually occur in the "clear length" of tall trees or that central portion between the swollen base and the crown which is devoid of branches; whereas smaller tracheids are characteristic of suppressed branches and of the physiologically dwarfed stems of depauperate plants.



TEXT FIGURE 1. Graphs illustrating variations in length of tracheary elements in passing from the innermost to the outermost secondary xylem. (A) Root: 2½ inches in diameter and 120 years old. (B) Root: 12 inches in diameter and 450 years old. (C) Stem: 5 feet in diameter and 420 years old, at stump height. (D) Branch: 1¾ inches in diameter and 130 years old, from the crown of a huge old tree. Each point on the graphs represents an average of 100 measurements.

As indicated in *Text fig. 1,* the tracheary elements of the redwood fluctuate in length much as they do in other representatives of the Coniferæ, but the range of variability tends to be greater than in smaller

and shorter-lived species. In the material examined by us, the tracheids vary from less than a millimeter to more than a centimeter in length. The longest cells occur in roots, *Text fig. 1, A* and *B*, and the clear length of tall stems, whereas shorter cells are formed in branches, *Text fig. 1, D*, and in suppressed stems.

The tracheids of *Sequoia sempervirens* fluctuate from less than 10 μ to more than 100 μ in diameter. In radial strips from the clear lengths of huge mature trees, the average tangential diameter of the tracheids commonly varies from approximately 20 μ in the innermost rings to 60 μ in the outer growth layers, *Figs. 1, 4,* and *5*. In old suppressed branches, on the contrary, the differences in diameter, 18 to 24 μ, may be scarcely detectable, *Figs. 7-9*. In the roots of the Abietineæ, the widest tracheids frequently occur in close proximity to the primary elements; whereas in the redwood the tracheary cells commonly are smaller in the innermost rings, *Figs. 15* and *16*, but rapidly attain dimensions which are comparable with those of the tracheids of the outermost rings of old stems (compare *Figs. 3-5*, and *10*).

The form of the tracheids, as seen in transverse sections, varies from square or rectangular, *Figs. 2* and *5*, to asymmetrically pentagonal or hexagonal, *Figs. 4, 10,* and *16*, and in typical "compression wood" to oval or nearly circular, *Figs. 6* and *47*. Radially narrow rectangular forms are characteristic of the outermost tracheids of wide rings and of the entire latewood of such growth layers as those illustrated in *Figs. 4, 5, 8,* and *10*. Radially elongated forms are of common occurrence in large-celled earlywood of old stems and roots, *Figs. 4, 6, 10,* and *16*. Owing to variations in the size of tracheids and in the thickness of their walls, specific gravity is not a constant for either earlywood or latewood.

INTER-TRACHEARY PITTING

The more conspicuous variations in the size, form, number, and orientation of the bordered pits in the radial walls of the tracheids, *Figs. 20-30*, are more or less closely correlated with fluctuations in the size of these cells and in the thickness of their walls. In other words, the bordered pits tend to become larger and more numerous as the tracheids increase in radial diameter in an expanding stem or root (compare *Figs. 20* and *25, 26* and *30, 28* and *29*); but, within each growth layer, they decrease in size and number in passing from the larger thin-walled elements of the earlywood to the smaller thick-walled cells of the latewood. The pits commonly tend to be more numerous toward the overlapping ends of the tracheids and in those portions of the radial walls which are in contact with the terminal portions of

adjoining tracheids. Furthermore, the pits tend to be more numerous in relatively narrow rings than in unusually wide growth layers. Therefore, in studying variations in tracheary pitting, it is essential not only to compare homologous parts of the growth layers, but also equivalent areas of the walls of the tracheids.

The radially narrow tracheids of the latewood and the earlywood tracheids of the inner growth layers of stems and branches usually have a single row of small bordered pits; i.e., a single bordered pit is formed over each of the more or less conspicuous primary pit-fields, *Fig. 25.* On the contrary, the large earlywood tracheids of old stems and roots may form from 1-4 large bordered pits over each of the transversely elongated primary pit-fields, *Figs. 20-23.* Where the pits are approximated vertically, *Fig. 20,* the crassulæ[1] ("Bars of Sanio") are rodlike, and the primary walls have a scalariform appearance; where they are more widely spaced, *Figs. 21-23,* the crassulæ tend to be curved about the upper and lower margins of the oval primary pit-fields. "Forked," "split," or "fused" and very broad crassulæ, *Figs. 21* and *25,* are likewise of frequent occurrence.

Although the tracheary pitting of the redwood is commonly of the so-called opposite type, it readily passes over into typical alternating and closely crowded arrangements. When this change occurs, primary pit-fields and crassulæ are eliminated, *Figs. 27-29,* except in the case of such transitional or intermediate types of pitting as are illustrated in *Fig. 21.* In the redwood, as in *Cedrus* and other representatives of the Abietoideæ, the alternating orientation is of more frequent occurrence in roots than in stems; and, in the case of the aerial portions of the tree, in tracheids in close proximity to the primary wood and in the outer narrow rings of very old huge stems than in intervening tissue.

The individual bordered pits, which vary in diameter from 5-25 μ, may be circular, *Figs. 22, 23,* and *25,* oval or transversely elongated, *Fig. 30,* or flattened on one or more sides by close crowding, *Figs. 20, 21, 27,* and *29.* Many of them have conspicuously indented or notched contours, *Figs. 22, 23, 25,* and *26.* The pit apertures may be circular, oval, lenticular, or slitlike; their form and orientation fluctuating with variations in the physical structure (Zimmermann, 31) and thickness of the secondary walls of the tracheids.

When thin, transverse sections of normal tracheids are examined in polarized light with crossed nicols, the secondary walls are seen to con-

[1]In this paper, we have adopted the terminology proposed by the Committee on Nomenclature of the International Association of Wood Anatomists (6).

sist of three distinct layers, *Fig. 46*: (1) a thin, outer layer which transmits polarized light and is brilliant, (2) a thin, inner brilliant layer, and (3) an intervening layer of varying thickness which is dark or transmits less light than the inner and outer layers (Dippel, 7). The transmission of polarized light is closely correlated with the orientation of micellæ or chains of cellulose molecules. Where these are arranged parallel to the long axis of a tracheid, a layer appears dark in cross sections of the xylem; where they are oriented nearly at right angles, a layer is brilliant. The transmission varies at intervening angles. In other words, the micellæ of the thin inner and outer layers of the secondary wall tend to be oriented more nearly at right angles to the long axis of the cell, whereas those of the central layer are arranged either longitudinally or diagonally.

Variations in the thickness of the secondary wall are closely correlated with fluctuations in the width of the central layer, rather than of the inner and outer layers, *Fig. 46*. Where the central layer is relatively thin or inconspicuous, as, for example, in the large earlywood tracheids of old stems and roots, the pit apertures tend to be circular or transversely elongated; whereas in tracheids with thicker walls the apertures usually are lenticular or slitlike and are oriented either longitudinally or diagonally. The outlines of the apertures of a pit-pair may be superimposed or "crossed," the latter condition occurring where the orientation of lenticular or slitlike pits is diagonal. The secondary wall of the tracheids of "compression wood" differs from that of normal tracheids in having a wide inner layer, *Fig. 47*, which is coarsely and diagonally striated (Hartig, 16). This layer develops more or less numerous spirally arranged cracks during dehydration, and the apertures of the pits become extended far beyond the outlines of the borders.

The torus—i.e., the thicker central portion of the pit-membrane which stains intensely with Ruthenium Red or Haidenhain's Hæmatoxylin—varies markedly in size, form, and thickness. It may be absent, small and of irregular form, *Fig. 30*, or large, thick and disk-like, *Fig. 26*. Frequently it is conspicuously punctate, and the surrounding portion of the pit-membrane commonly tends to be more or less clearly striated or reticulated.

Bordered pits may develop in the tangential walls of the tracheids of both earlywood and latewood, particularly in the case of the narrower growth layers of old stems and roots. The tangential pits of the earlywood are larger, of sporadic distribution, and tend to have circular or oval apertures; whereas those of the latewood are smaller,

more numerous and uniformly distributed, and have lenticular or slit-like apertures. Crassulæ and primary pit-fields are absent in the tangential walls of the tracheids, but tori may be present in the bordered pits.

WOOD PARENCHYMA

The wood parenchyma of the redwood, as of many other Coniferæ, varies greatly in different parts of a single tree. It may be abundant and diffused throughout most of an annual ring, *Figs. 1, 7, 8,* and *11,* aggregated into more or less conspicuous zones, *Figs. 9* and *13,* confined to the latewood, *Fig. 2,* or much reduced in amount, *Figs. 4, 5, 6,* and *10.* Not infrequently it tends to be more abundantly developed in the inner than in the narrow outer rings of old stems and roots.

The individual strands of wood parenchyma fluctuate in length and in tangential diameter much as do the surrounding tracheary elements. This is due to the fact that both categories of cells are derived from the same fusiform initials, and therefore increase in size as the cambial initials become longer and wider. Minor differences in the length and cross-sectional area of parenchyma strands, as contrasted with tracheids, are due to differences in enlargement during tissue differentiation. The derivatives of the fusiform initials which divide transversely to form strands of wood parenchyma, do not elongate during differentiation of the xylem, whereas young tracheids may do so. The radial expansion of the parenchyma strands frequently tends to be less than that of the adjoining tracheids, but in the inner rings of roots the cross-sectional area of the parenchymatous elements may at times exceed that of the largest tracheids.

RAYS

Fisher (9), Essner (8), and Jaccard (18) have shown that rays vary in size and in number per unit area not only within different parts of a single tree but also within different parts of a single growth layer. In the redwood, as in the Coniferæ studied by Essner, the rays are smaller and more numerous, *Fig. 33,* in the innermost rings of stems and branches than in subsequently formed tissue, *Figs. 31, 32, 35-37.* This is due in part to an increase in height of the rays with concomitant ray-fusions, in part to an increase in the tangential diameter of the intervening tracheids, and in part to other factors. The height and width of the rays and the number of rays or ray cells per unit area are not constants, however, even in the outer growth layers of roots, branches, and stems, *Figs. 31, 32, 35-37.* The maximum height of the rays varies from a few cells to more than 75 cells, and the maximum

width from uniseriate to biseriate or triseriate and occasionally to multiseriate.

The individual ray cells fluctuate in size and form in different parts of a single tree and in homologous parts of different trees. The length, i.e., the radial dimension, of the ray cells varies from less than 35 μ to more than 500 μ; the depth, i.e., the vertical dimension, from less than 16 μ to more than 70 μ; and the width, i.e., the tangential dimension, from less than 9 μ to more than 40 μ. In general, the ray cells tend to be longer in earlywood than in latewood, in wide rings than in narrow ones, and in outer growth layers than in the innermost ones. Roots and the larger-celled growth layers of old stems tend to have broadly oval or "squarish" ray cells as seen in tangential sections, *Figs. 31, 36,* and *61;* whereas branches and the smaller-celled inner growth layers of stems commonly have narrower ray cells, *Figs. 32, 33, 35,* and *62,* in which the vertical dimension exceeds the tangential dimension. The ray cells, as seen in radial longitudinal sections of the xylem, may be uniformly rectangular or somewhat tapering in outline, with curved or diagonally oriented end walls. Furthermore, the marginal cells of the rays may be of approximately the same height as the central cells, or they may be much larger and provided with conspicuously curved outer walls.

PITS BETWEEN TRACHEIDS AND RAY CELLS

The ray cells of the redwood, as of the Taxodiaceæ, Araucariaceæ, Taxaceæ, Podocarpaceæ, Cupressaceæ, and Cephalotaxaceæ,[1] are provided with a more or less thickened primary wall, but do not form a true secondary wall such as is a characteristic feature of tracheary cells and of the rays of the Abietoideæ and most arborescent dicotyledons. This primary wall is derived directly from the ray initials of the cambium and is, in fact, a more or less modified cambial wall. As in the case of the ray initials, it is provided with more or less conspicuous primary pit-fields and plasmodesmata, i.e., sieve pitting, and tends to be conspicuously thickened at the angles of the cells where in contact with intercellular spaces, *Figs. 61,* and *62.* Simple pits and pits to intercellular spaces, which are characteristic features of the ray walls of the Abietoideæ, are entirely absent.

The presence of a true secondary wall in the rays of the Abietoideæ and its absence in the rays of the Taxodiaceæ, Cupressaceæ, etc., are of fundamental significance in any discussion of ray pitting. For

[1]Pilger's (25) nomenclature for the principal sub-groups of the Coniferæ is used throughout this paper.

example, there is at times a certain superficial resemblance between the end walls of the ray cells of *Juniperus* and those of *Cedrus, Abies,* or *Tsuga*. In *Juniperus* the investigator is concerned with deeply depressed primary pit-fields in primary walls, whereas in *Cedrus, Abies,* or *Tsuga* he is concerned with simple pits in secondary walls, i.e., entirely distinct morphological structures. In the case of pits in the "crossing field" or "tracheid field" of the rays of *Abies* or *Cedrus,* the investigator is dealing with half bordered pit-pairs; whereas in the rays of *Juniperus* or *Sequoia,* he is dealing with bordered pits which have no complementary simple pits on the ray side. The pit membranes are double structures formed by the wall of the ray and the adjacent primary wall of the tracheid, just as the tori and pit membranes of paired bordered pits are formed by the two adjacent primary walls of the tracheids.

The tracheary pits, which are visible through the crossing fields of the ray cells of the redwood, *Figs. 38-45,* vary in number from one to more than 20; in diameter, from less than 5 μ to more than 15 μ; in form, from circular or oval to asymmetrical; and in orientation from horizontal or vertical rows to diagonal or irregular groupings. The pit apertures, *Figs. 38-45,* may be slitlike, lenticular, or so much enlarged that the pit borders are more or less completely eliminated. Fusion of pit apertures, *Fig. 40,* or of both pit apertures and pit chambers, *Fig. 39,* are of not infrequent occurrence. Pit apertures may be oriented parallel to the long axis of the ray cells, *Fig. 38,* parallel to the long axis of the tracheids, *Fig. 45,* or in various diagonal positions, *Figs. 39-44.* As in the case of inter-tracheary pitting, variations in the orientation of the pit apertures are closely correlated with fluctuations in the thickness of the secondary wall of the tracheids and in the physical structure of its constituent layers.

The more conspicuous variations in the number and orientation of the pits within the outlines of a crossing field are correlated with fluctuations in the radial diameter of the tracheids and in the height of the ray cells. In other words, low ray cells in contact with narrow tracheids, *Figs. 39, 41,* and *43,* tend to have fewer pits per crossing field than similar ray cells in contact with wider tracheids, *Figs. 38, 40, 42,* and *45,* or than high ray cells in contact with either narrow or wide tracheids, *Fig. 44.* Where the crossing field is much elongated radially, the pits tend to occur in horizontal rows, *Fig. 38;* but where it is vertically elongated, the pits usually are oriented in vertical rows, *Fig. 44.* Thus, in the outer growth layers of old stems and roots, the orientation of the pits shifts from horizontal to vertical in passing from the wide tracheids of the earlywood to the narrow tracheids of the latewood.

SIEVE PITTING OF PARENCHYMATOUS CELLS

The wood parenchyma cells of the redwood resemble the ray cells in having a primary wall of varying thickness but no true secondary wall. Thus, in the case of both wood parenchyma and rays, the primary walls of adjoining parenchymatous elements are provided with more or less numerous plasmodesmata which may be evenly and uniformly distributed or aggregated in primary pit-fields. Where the plasmodesmata are numerous and evenly distributed, *Fig. 48*, as in the end walls of many ray cells and wood parenchyma cells, the walls are relatively smooth in sectional view, *Fig. 49*. On the contrary, where the plasmodesmata are aggregated in primary pit-fields, *Figs. 50, 51, 53, 54, 56, 57*, and *58*, the walls appear to be beaded or unevenly thickened in sectional view, *Figs. 52, 55*, and *59*. It should be emphasized in this connection, however, that where the walls are as tenuous as they are in the primary pit-fields (white areas) of *Figs. 54, 56, 57*, and *58*, it is difficult to demonstrate the delicate sieve structure in photomicrographs.

The primary pit-fields vary in size, form, depth, number, and distribution in the various surfaces of the parenchymatous elements and in different parts of the tree. As previously stated, there may be a single large sieve field, *Fig. 48*, in the end walls of the parenchymatous elements or a varying number of more or less discrete sieve areas which are located in primary pit-fields, i.e., thinner areas of the primary walls. The former condition tends to be of more frequent occurrence in thin-walled than in thick-walled cells, in the narrow outer rings of old stems and roots than in the inner growth layers, and in ray parenchyma than in wood parenchyma. The primary pit-fields usually are more widely spaced in side walls, *Figs. 58* and *59*, than in end walls, *Figs. 54-56;* in the side walls of much elongated ray cells than of shorter ones; and of earlywood than of latewood. Furthermore, where the ray cells are very broad, fewer primary pit-fields are visible in a single focal plane of a radial section than where the ray cells are narrower. It should be emphasized, in this connection, that the smoother appearance of the upper and lower ray walls in radial sections of the redwood, as contrasted with similar sections of the Abietoideæ, is due, in large part, to the absence of pits to the intercellular spaces.

TRAUMATIC RESIN CANALS

The cambium of the redwood is extremely sensitive to traumatic stimuli and to abnormal environmental influence and tends to form arcs of resin canals, *Figs. 8, 12, 14-19*, which extend considerable dis-

tances beyond the principal focus of stimulation. In other words, an injury to the crown may induce the formation of resin canals not only in the injured branches, but in the stem as well. The cambium of *Sequoia sempervirens* differs, however, from that of *Sequoia gigantea,* and particularly from that of the various species of *Cedrus,* in not forming horizontal resin canals.

The resin-canals of the redwood vary greatly in size and shape, in the character and abundance of the specialized cells which jacket them, in the presence or absence of tylosoids, and in the position of the canals within the growth layers, *Figs. 14-19.* The schizogenous cavities may be minute, *Fig. 15,* or relatively large, *Fig. 14.* They may be angular, *Fig. 15,* oval, circular, *Fig. 16,* slit-like, *Fig. 17,* or irregular, *Fig. 14.* They may have a conspicuous and clearly differentiated epithelium, *Figs. 16* and *19,* or irregular jacketing mixtures of strand tracheids and parenchyma, *Figs. 14, 17,* and *18.* The location of the resin canals is determined by the season of the year at which the abnormal stimulus occurs. Thus, the canals may be located in the first-formed portion of the earlywood, *Fig. 18,* in the outer portion of the latewood, *Figs. 14, 15,* and *17,* or in various intermediate positions, *Figs. 16* and *19.* They tend, in general, to be of more frequent occurrence in the branches and roots of old trees than in the clear length of the stem. It is significant, however, that in certain parts of the range of the redwood, the crowns of trees growing in exposed situations are injured each year by severe storms which occur at specific periods during the growing season. The stems of such trees frequently form arcs or rings of resin canals in a large proportion of the successively formed growth layers, *Fig. 12.*

STRAND TRACHEIDS

The redwood exhibits a strong tendency to form numerous strand tracheids not only in close proximity to traumatic resin canals, but also upon the outer surface of the latewood of growth layers or parts of growth layers which are devoid of resin canals, *Fig. 31.* Not infrequently they are developed with such regularity in successively formed growth layers as to appear of normal occurrence, but are in all probability due to some periodically recurring environmental stimulus.

RAY TRACHEIDS

Ray tracheids are of extremely uncertain and sporadic distribution in the redwood (Gordon, 13; Holden, 17). They may be abundantly developed in stems which exhibit no evidences of wounding and may be entirely absent in severely injured specimens. They may be aggre-

gated in a single independent radial row or erratically distributed along the margin of the rays. Their size and shape are variable, and their walls may be smooth or provided with helical thickenings.

CONTENTS OF PARENCHYMA AND "RESINOUS" TRACHEIDS

The ray cells and wood parenchyma strands of the redwood commonly contain a varying amount of ergastic material which varies in color from light yellow or orange to reddish-brown, dark red, or nearly black. It may be distributed in irregular masses, in large globules, or in finely granular or alveolar forms. In the heartwood of old roots, and of many stems and branches, not only do the walls of the tracheids become saturated with more or less of this material, but it exudes into the lumina, where it frequently forms septa, or plugs, which appear spool-shaped in sectional view, *Fig. 60*. Tracheids which contain such biconcave septa are commonly referred to as resinous tracheids (Penhallow, 24; Record, 26).

DISCUSSION

As stated in our introduction, systems of classifying and identifying the woods of conifers and dicotyledons have developed largely through trial and error. In other words, each investigator assembles, or has access to, a collection of relatively small samples of the wood of various genera and species. These specimens are sectioned and are laboriously and minutely studied in a search for structural differences which may be utilized in the construction of keys. Each investigator finds that certain of the diagnostic criteria used by his predecessors are unreliable and replaces them by others of putatively greater conservatism.

The inherent difficulty in this method of approaching the problem is that available collections of woods are extremely heterogeneous assemblages of fragmentary specimens from different sources. Samples of the wood of one species or genus may be from old virgin forest trees, those of another species or genus from young second-growth forests, and those of a third from trees planted in botanic gardens or arboreta. Therefore, the prevailing conception of the structural characteristics of the xylem of any particular species or genus depends upon chance, i.e., upon the types of specimens which happen to be available in existing collections. Students of commercial timbers naturally confine their attention to the merchantable part of the tree; but the parts of the tree which eventually reach the market vary with the species, with the uses to which different woods are put, and with many other factors.

In the case of *Sequoia sempervirens*, the properties of the wood and the commercial requirements are such that the outer parts of the clear lengths of old slowly growing trees are prized for industrial utilization. Therefore, it is not surprising that in such manuals as those of Koehler (20) and Brown (5) wood of the general type shown in *Fig. 4* is selected for study and illustration. It is significant, however, that the detailed anatomical descriptions of Penhallow (24) and of other botanists and paleobotanists appear to be based largely upon the investigation of similar material. The prevailing conception of the anatomical characteristics of *Sequoia gigantea* likewise is based upon the study of material from the outer portions of huge old stems, whereas that of other species and genera frequently is derived from an examination of specimens from young or immature stems.

Our detailed study of the redwood, and our preliminary observations upon the range of structural variability in various representatives of the Pinaceæ, Araucariaceæ, Taxaceæ, Podocarpaceæ, Taxodiaceæ, and Cupressaceæ, indicate that most, if not all, of the anatomical characters which have been utilized for diagnostic purposes fluctuate more or less, not only in trees grown under markedly different environmental conditions, but also within different parts of a single individual. This is as true of such supposedly conservative qualitative characters as form and orientation of pits, or of pit apertures, as of such quantitative characters as width of annual rings, dimensions of cells, or number of rays per unit area. In general, the range of variability tends to be greater in different parts of a single large mature tree than in homologous parts of different trees of the same species. There are significant anatomical differences not only in comparable parts of stems, roots, and branches, but also in growth layers formed at successive intervals during the development of each of these organs. Thus, although wood from the outer parts of huge old stems may resemble that of the root, it usually differs considerably from the wood of younger stems, of branches, or of seriously suppressed or dwarfed stems.

It is evident, in view of such facts as these, that, if the problem of classifying and identifying the woods of gymnosperms and angiosperms is to be attacked from a thoroughly scientific point of view, collections of authentic specimens must be assembled, not only from different genera, species, and varieties, but also from different parts of mature trees and from trees growing under different environmental conditions. The available anatomical data—tabulated from miscellaneous collections and without due regard to significant developmental, physiological, and ecological factors—do not provide a reliable basis for dis-

tinguishing the woods of most closely related species or even of many remotely related ones. This is particularly true of fossilized specimens which may be derived from any part of the tree and where such macroscopic aids as color, odor, gloss, hardness, etc., are evanescent. Thus, although it is possible to differentiate the wood of *Sequoia* from that of the Taxaceæ, Araucariaceæ, Abietoideæ, and Pinoideæ, and to determine, for example, that *Sequoia Penhallowii* is, in reality, a representative of the Abietoideæ, it is difficult to distinguish the wood of *Sequoia,* in all cases, from that of the Podocarpaceæ, Cupressaceæ, and other genera of the Taxodiaceæ. As indicated on preceding pages, the pitting of rays and of wood parenchyma—upon which Penhallow (24), Gothan (14), Kräusel (21), Kanehira (19), Slyper (30), and others place so much reliance—may fluctuate markedly within a single tree or species. For example, the pits in the crossing fields of the rays (earlywood) of the redwood vary from "taxodioid" to "cupressoid," "podocarpoid," or "glyptostroboid," depending upon the source of the wood that is selected for investigation. Similarly, the structure of the end walls of the wood parenchyma, as seen in tangential longitudinal sections of the xylem, may be smooth or conspicuously beaded (Taxodium type), depending upon the part of the tree from which the wood is cut.

In the seventh paper of this series, it was shown that such putative transitional Mesozoic Coniferæ as *Protopiceoxylon, Planoxylon, Thylloxylon,* and *Protocedroxylon* fall within the range of structural variability of living representatives of the Abietoideæ. These genera are characterized, as are *Cedrus, Keteleeria, Abies, Tsuga, Pseudolarix, Larix, Pseudotsuga,* and *Picea,* by ray cells which form true secondary walls. The question arises, accordingly, whether other representatives of the hypothetical transitional Araucariaceæ, which do not exhibit this type of ray structure, fall within the range of anatomical variability of the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ.

The salient arguments for regarding *Brachyoxylon, Paracedroxylon, Telephragmoxylon, Anomaloxylon, Paraphyllocladoxylon,* and *Paracupressinoxylon* as araucarians in disguise rather than as representatives of the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ are the reputed absence of crassulæ and the occurrence, particularly towards the ends of the tracheids, of so-called araucarian pitting. Emphasis is frequently placed, in addition, upon the occurrence of "resinous" tracheids and of clusters of medullary stone cells, and upon the absence of wood parenchyma and of clearly defined growth layers.

Clusters of sclerides or stone cells, *Fig. 34,* are of not infrequent occurrence in the pith of the redwood and have been reported in

Torreya, Podocarpus, Dacrydium, and *Cryptomeria* (Seward, 28). Typical "resinous" tracheids, *Fig. 60,* are abundantly developed in many specimens of *Sequoia sempervirens* and are known to occur in *Pinus* and other conifers exclusive of the Araucariaceæ. Wood parenchyma may be entirely absent in specimens of the wood of various representatives of the Taxodiaceæ and Podocarpaceæ and may be present in the secondary xylem of living representatives of the Araucariaceæ. Similarly growth layers may be strikingly differentiated in the Araucariaceæ and feebly developed or absent in the Podocarpaceæ, Taxodiaceæ, and Cupressaceæ. Furthermore, contiguity and alternation of tracheary pitting is by no means an infallible criterion of araucarian affinity. We have shown that in the redwood, as in *Cedrus* and other representatives of the Abietoideæ, the tracheary pitting shifts at times from an opposite to an alternating orientation and from a widely spaced to a closely crowded arrangement. Such changes in the arrangement of the bordered pits tend to occur most readily at the ends of the tracheary cells. It should be emphasized, in addition, that where the pits shift to the so-called araucarian orientation, crassulæ and primary pit-fields are more or less completely eliminated. An investigation of a wide range of Podocarpaceæ, Taxodiaceæ, and Cupressaceæ reveals not only that contiguity and alternation of tracheary pitting are of more frequent occurrence than has been hypothesized, but also that where the pits are in opposite or widely spaced arrangement, the crassulæ may be so tenuous that they can be demonstrated only after delicately controlled differential staining. Primary pit-fields and crassulæ which are clearly visible in sapwood may be completely obscured during the transformation of sapwood into heartwood. To assume that these delicate structures of the primary walls are preserved in visible form in all material and under all conditions of fossilization is illogical.

It is evident, accordingly, not only that there are no convincing arguments for assuming that the various Paracupressinoxyla and Brachyphylleæ are transitional or ancestral types of Araucariaceæ, but also that most of them fall within the potential ranges of variability of the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ. A number of them, obviously, exhibit combinations of anatomical characters which occur in living representatives of the genus *Sequoia.* For example, *Telephragmoxylon* was instituted for woods of putative araucarian affinities which are characterized by having strand tracheids upon the outer surface of the latewood. We have shown that the redwood has a pronounced tendency to form strand tracheids and that, in trees from

certain parts of the range of the species, these strand tracheids are present upon the outer surface of many successive growth layers and thus appear to be of normal occurrence. Not only are typical schizogenous resin canals, "resinous" tracheids, and clusters of medullary stone cells of frequent occurrence in the redwood, but wood parenchyma may be greatly reduced in amount and practically eliminated from certain specimens. Thus, in so far as one may judge from published descriptions and illustrations, both species of *Telephragmoxylon* fall within the range of structural variability of *Sequoia*, and may, in fact, be remains of this genus or of some closely related one.

It should be emphasized in conclusion that, in the present status of our knowledge concerning the variability of diagnostic criteria and in view of the difficulty of accurately determining the generic and even the sub-family affinities of many specimens, specific names as applied to fossil woods have no significance other than as aids in designating particular specimens. The word, "species," must be used for the present in an entirely different sense from that in which it is employed in systematic botany. Many of the supposedly distinct "species" of fossil woods may actually have been derived from the same species or even from different parts of a single tree. Conversely, specimens which are referred to a particular "species" may actually have been derived from different species or genera. It should not be inferred from this, however, that the problem of identifying plants by the structure of their secondary xylem is necessarily a hopelessly difficult one. Not only is there the possibility of ultimately finding structures or characters which are present in one genus or species and entirely absent in others, but the ranges of structural variability vary in different plants. Thus, the *combinations* of structural characters that occur in specific parts of the tree may fluctuate from species to species.

SUMMARY AND CONCLUSIONS

1. A detailed investigation of the secondary xylem of the redwood demonstrates that most anatomical characters fluctuate considerably not only in trees grown under markedly different environmental conditions but also within different parts of a single tree. This is as true of such supposedly conservative qualitative characters as form and orientation of pits, or of pit apertures, as of such quantitative characters as width of annual rings, dimensions of cells, or number of rays per unit area.

2. In general, the range of variability tends to be greater in different parts of a single, large mature tree than in homologous parts of

different trees. There are significant differences not only in comparable parts of stems, roots, and branches, but also in growth layers formed at successive intervals during the development of each of these organs.

3. In the redwood, as in other conifers, the cambial initials and their derivatives increase in size for a varying period of years, after which they tend to remain constant except where deviations are induced by various modifying factors. The cells of roots and of the outer parts of the clear lengths of huge old stems tend to be larger than those of young stems, of physiologically dwarfed stems, or of branches.

4. Many of the salient variations in the size, form, number, and orientation of pits and of primary pit-fields are correlated with such fluctuations in the size of cells and in the thickness and physical structure of their walls. Thus, different combinations of anatomical characters tend to prevail in different parts of a tree and in tissues formed under varying growth conditions.

5. A preliminary study of the ranges of structural variability in various representatives of the Coniferæ indicates that although it is possible to differentiate the wood of *Sequoia* from that of the Taxaceæ, Araucariaceæ, Abietoideæ, and Pinoideæ, it is difficult to distinguish it in all cases from that of the Podocarpaceæ, Cupressaceæ, and other genera of the Taxodiaceæ.

6. Characters which have been interpreted as indications of araucarian affinities—i.e., contiguity and alternation of tracheary pitting, absence of crassulæ and of wood parenchyma, occurrence of "resinous" tracheids and of clusters of medullary stone cells, etc., are of not uncommon occurrence in the redwood and other representatives of the Podocarpaceæ, Taxodiaceæ, and Cupressaceæ.

7. There are no convincing arguments for assuming that the various Paracupressinoxyla and Brachyphylleæ are transitional or ancestral types of Araucariaceæ, rather than forms related to the Podocarpaceæ, Taxodiaceæ, or Cupressaceæ. A number of them exhibit combinations of anatomical characters which fall within the potential range of structural variability of the genus *Sequoia*.

8. Systems of classifying and identifying the woods of gymnosperms and angiosperms have developed largely through trial and error. Available anatomical data—tabulated from miscellaneous collections of more or less fragmentary specimens and without due regard to significant developmental, physiological, and ecological factors—do not provide a reliable basis for distinguishing the woods of most closely related species and of many remotely related ones.

9. If the problem of classifying and identifying the woods of gymnosperms and angiosperms is to be attacked from a thoroughly scientific point of view, collections of authentic specimens must be assembled, not only from different genera, species, and varieties, but also from different parts of mature trees and from trees growing under different environmental conditions.

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DESCRIPTION OF PLATES

PLATE 99

Sequoia sempervirens

Figs. 1-5. *Stem.* Transverse sections of the xylem, showing structural details of growth layers at successive intervals between the pith and bark of a large stem. × 32.

PLATE 100

Sequoia sempervirens

Fig. 6. *Stem.* Transverse section of the xylem from the outermost portion of an old tree, showing wide layer of "compression wood." × 32.

Figs. 7 & 8. *Branch.* Transverse sections of the xylem, showing growth layers from the inner and outer parts of an old branch. × 32.

Fig. 9. *Branch.* Transverse section of the xylem from the under side of an old branch, showing "compression wood." × 32.

Fig. 10. *Root.* Transverse section of the xylem of an old root. × 32.

Plate 101

Sequoia sempervirens

Fig. 11. *Stem.* Transverse section of the xylem of a young vigorous tree, showing wide growth layer and gradual transition between earlywood and latewood. × 17.

Fig. 12. *Stem.* Transverse section of the xylem, showing traumatic resin canals in the latewood of three successive growth layers. × 17.

Fig. 13. *Stem.* Transverse section of the xylem, showing wide growth layer formed after a prolonged period of suppression. × 17.

Plate 102

Sequoia sempervirens

Figs. 14, 17-19. *Stem.* Transverse sections of the xylem, showing various types of traumatic resin canals. × 54.

Fig. 15. *Root.* Transverse section of the xylem of a young root, showing traumatic resin canals. × 54.

Fig. 16. *Root.* Transverse section of the xylem of an old root, showing traumatic resin canals. × 54.

Plate 103

Sequoia sempervirens

Figs. 20-25. *Stem.* Radial longitudinal sections of the xylem, showing variations in the form and in the distribution of primary pit-fields, crassulæ, and bordered pits in thin-walled tracheids of varying diameters. × 255.

Figs. 27-29. *Root.* Radial longitudinal sections of the xylem, showing compressed and alternating arrangements of bordered pits. × 255.

Figs. 26 & 30. *Stem.* Radial longitudinal sections of the xylem, showing variations in the size and form of the torus. × 1680.

Plate 104

Sequoia sempervirens

Fig. 31. *Stem.* Tangential longitudinal section of the xylem, showing strand tracheids, rays, and bordered pits. × 54.

Fig. 34. *Stem.* Transverse section of the pith, showing cluster of stone cells. × 73.

Figs. 32, 33, 35-37. *Stem.* Tangential longitudinal sections of the xylem, showing common variations in the size and form of rays and of their constituent cells. × 54.

Plate 105

Sequoia sempervirens

Figs. 38-43, & 45. *Stem.* Radial longitudinal sections of the *first formed part* of the earlywood of various growth layers, showing variations in the size, form, number, and orientation of bordered pits in the "crossing fields" of the rays. × 1210.

Fig. 44. *Root.* Radial longitudinal section of the xylem of a young root, showing orientation of bordered pits in the crossing field of a ray. × 1210.

Fig. 46. *Stem.* Transverse section of the xylem, photographed with polarized light. × 965.

Fig. 47. *Stem.* Transverse section of "compression wood," photographed with polarized light. × 965.

PLATE 106

Sequoia sempervirens

Figs. 48 & 51. Tangential longitudinal sections of the xylem, showing surface views of the sieve pitting in the end walls of ray cells. × 500.

Figs. 50, 53, 54, 56, & 57. Transverse sections of the xylem, showing primary pit-fields and sieve pitting in the end walls of wood parenchyma. × 500.

Figs. 49, 52, 55. Tangential longitudinal sections of the xylem, showing sectional views of the end walls of wood parenchyma. × 500.

Fig. 58. Transverse section of the xylem, showing surface view of the wall of a ray cell. × 500.

Fig. 59. Tangential longitudinal section of the xylem, showing sectional view of the lateral walls of wood parenchyma. × 500.

Fig. 60. Radial longitudinal section of the xylem, showing "resinous tracheids." × 170.

Figs. 61-62. Tangential longitudinal sections of the xylem, showing details of ray structure. × 500.

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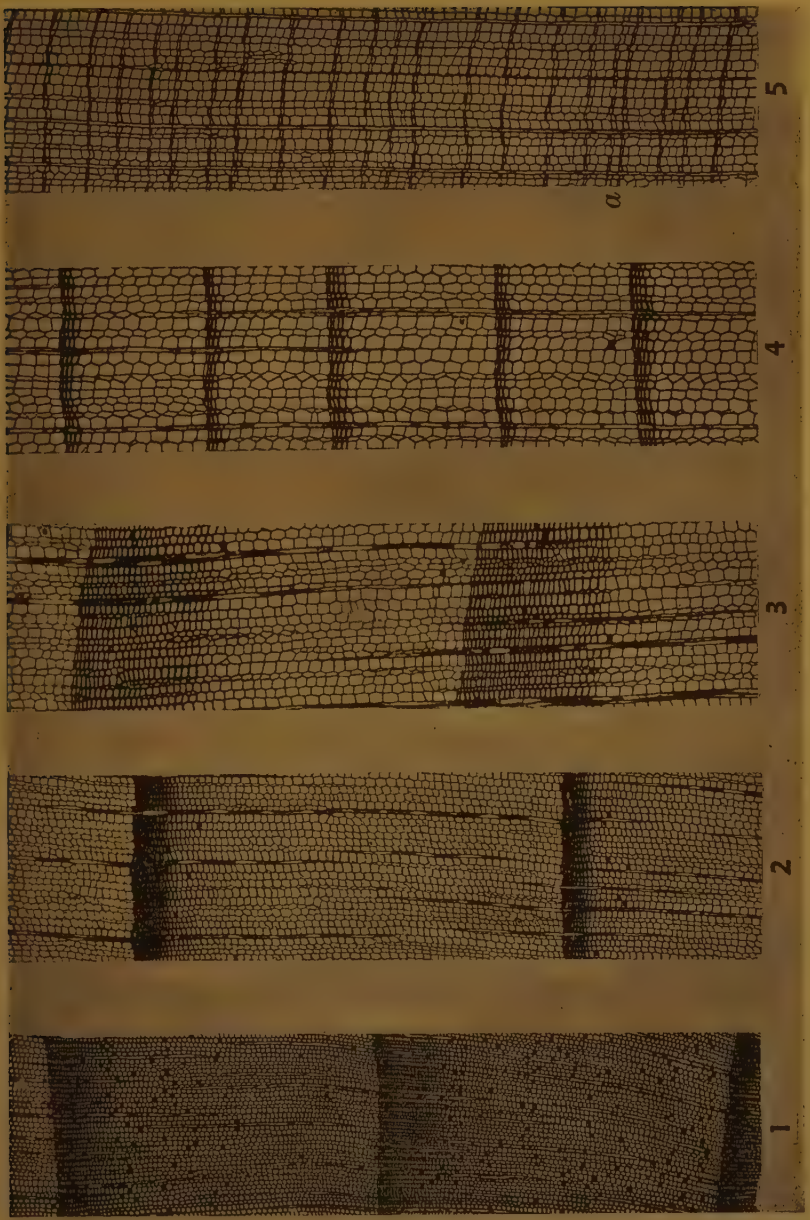
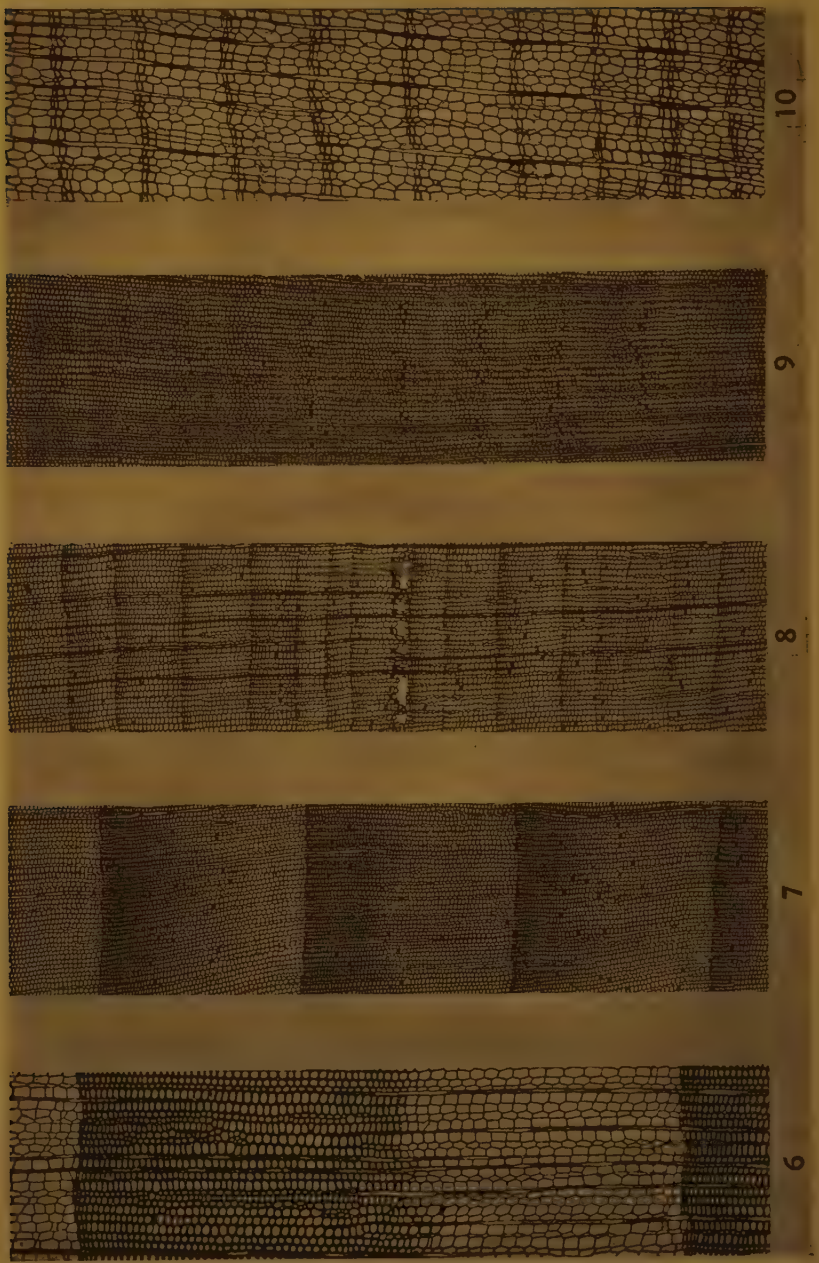


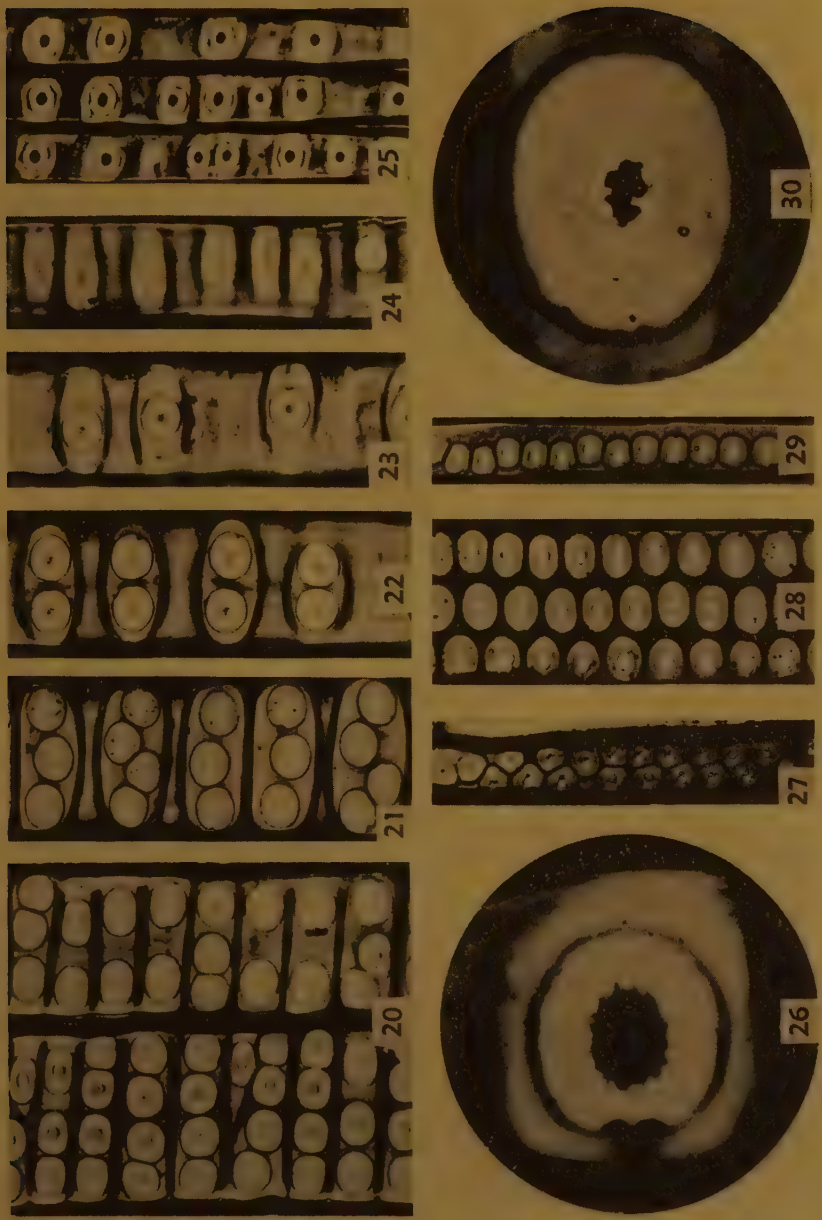
Structural Variability in the Redwood



Structural Variability in the Redwood

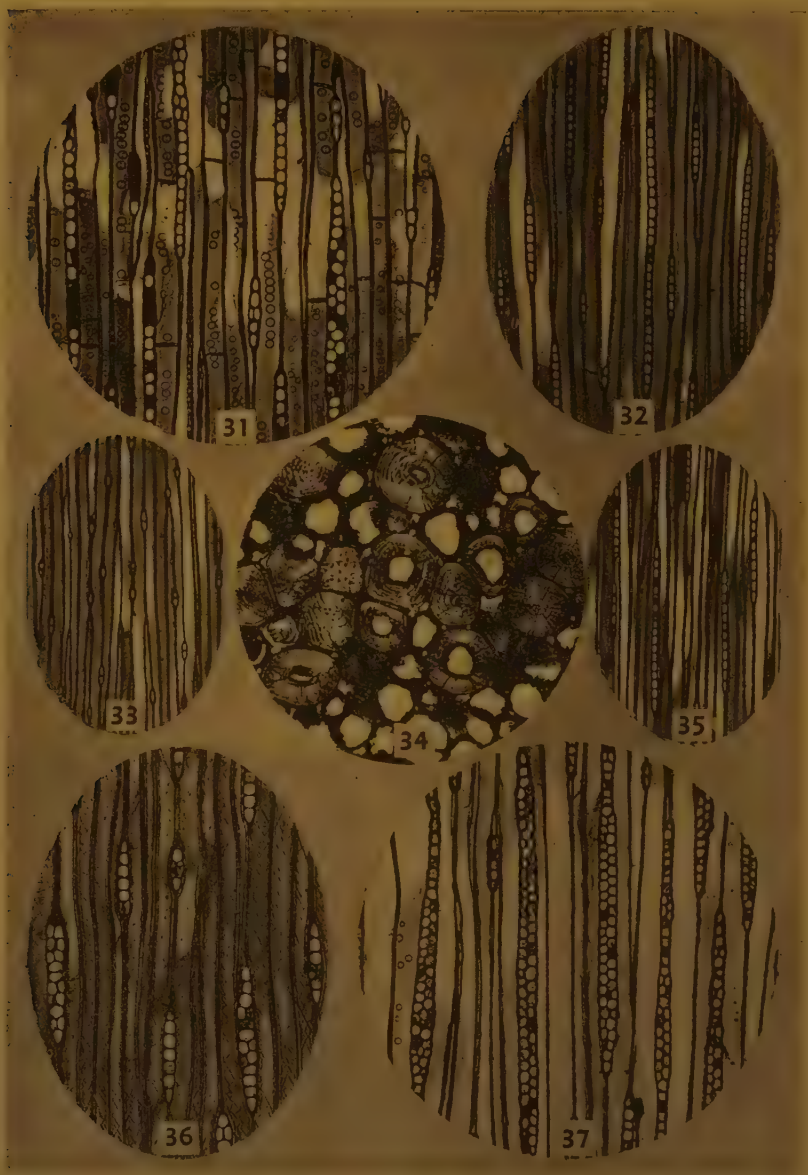
Structural Variability in the Redwood

Structural Variability in the Redwood



Structural Variability in the Redwood

The Heliotype Corp. Boston



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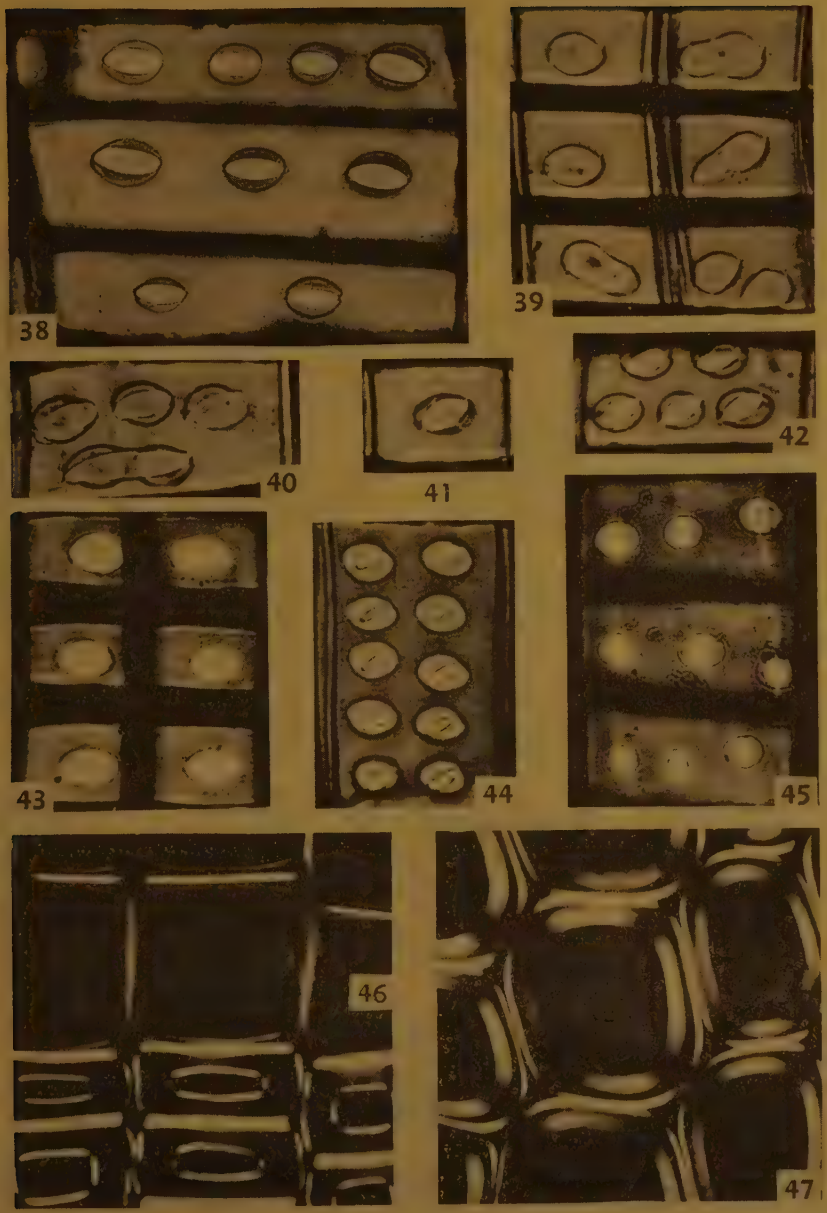

Structural Variability in the Redwood

THE HELIOTYPE CORP. BOSTON

Structural Variability in the Redwood

THE HELIOTYPE CORP. BOSTON

CHROMOSOMES OF THE CYCADALES

KARL SAX AND J. M. BEAL

With plates 107 and 108

THE CYCADS are the most primitive of the living gymnosperms and represent the surviving remnants of a line reaching back through the Mesozoic into the Paleozoic era. Nine genera, containing less than one hundred species, are recognized. Four of the genera occur exclusively in the western hemisphere and the other five in the eastern.

Of the western genera, *Zamia,* with twenty-six species, ranges from southern Florida to Chile. *Microcycas* is a monotypic genus and is found only in western Cuba. *Dioon,* with three species is found only in southern Mexico, and *Ceratozamia* with two species has about the same range as *Dioon.*

Of the eastern genera, *Cycas,* with eight species, ranges from Japan to Australia. *Macrozamia,* with nine species and the monotypic *Bowenia* occur in Australia. *Encephalartos,* with fourteen species and *Stangeria,* a monotypic genus, are found in southeastern Africa.

The basic chromosome number has been reported as 12 in most gymnosperms including the cycads, but recent work has shown that many of the earlier counts were incorrect (Sax and Sax 1933). The chromosome number and morphology in the gymnosperms is best obtained from the haploid endosperm cells, but it was so difficult to obtain female cones from most cycads that root tip preparations have been used almost exclusively. The root tips were fixed in acetic acid alcohol, and aceto-carmine smears were made from this material.

Material for the cytological investigation has been obtained from a number of sources. Female cones of *Zamia* were obtained from Mr. Robert Gray, superintendent of the Atkins Institution of the Arnold Arboretum at Soledad, Cuba. Dr. Edgar Anderson obtained root tips from several genera at the New York Botanical Garden, and some material was sent from the University of Pennsylvania by Dr. Conway Zirkle. Most of the material was obtained from Dr. Chamberlain's collection of cycads at the University of Chicago by the junior author.

So far as possible, we have followed Schuster's classification of the Cycadaceae (Engler, 1932). The following genera and species have been studied:—*Cycas revoluta* Thunb., *C. circinalis* L., *C. Rumphii* Miq., *Bowenia serrulata* André, *Macrozamia tridentata* (Willd.) Regel, *M. Miquelii* (F. Muell.) Schuster, *M. Moorei* F. Muell., *Stangeria paradoxa* Th. Moore, *Encephalartos Altensteinii* Lehmann, *Dioon spinulosum* Dyer, *Microcycas calocoma* (Miq.) A. DC., *Ceratozamia*

mexicana Brongn., *C. mexicana* var. *longifolia* (Miq.) Schuster, *Zamia floridana* A. DC. and two varieties of *Z. media* Jacq., var. *Gutierrezii* (Sauvalle) Schuster and var. *portoricensis* (Urban) Schuster. Two species collected as *Cycas* "Wadel" and as *Zamia pumila* L., could not be placed definitely according to Schuster's classification.

The chromosomes can be studied most readily in the "endosperm" cells. A few such preparations were obtained from female cones of *Zamia*. The chromosomes of most species examined were studied in aceto-carmine smears of root tips. In most cases it was possible to determine the chromosome number and morphology quite accurately. The chromosomes are large and in the smear preparations they are spread out in nearly the same focal plane. Photographs of the somatic chromosomes of several genera are shown in plate 107. The chromosomes of other genera and species are pictured in plate 108. Only two good division figures were obtained from *Bowenia* and in these the chromosomes were so widely scattered in smearing that it was impracticable to represent them in the photographs or drawings. *Dioon* also proved to be difficult, and in *D. edule* there appeared to be only 16 chromosomes in some figures, but these were not clear enough to establish a definite count. The chromosome numbers of *Zamia* species were obtained from both endosperm and root tips. A summary of the chromosome number and morphology of the different genera is shown in table I.

TABLE I.

CHROMOSOMES OF CYCADS

Species	Terminal fiber	sub-term. fiber	median fiber	Total 2 n.
Cycas revoluta	10	8	4	22
Cycas circinalis	10	8	4	22
Cycas Rumphii	10	8	4	22
Bowenia serrulata		6	12	18
Macrozamia tridentata	2	6	10	18
Macrozamia Miquelii	2	6	10	18
Macrozamia Moorei	2	6	10	18
Stangeria paradoxa	2	2	12	16
Encephalartos Altensteinii		4	12	16
Dioon spinulosum		10	8	18
Microcycas calocoma	22	2	2	26
Ceratozamia mexicana		4	12	16
C. mexicana var. longifolia		4	12	16
Zamia media				
var. Gutierrezii		4	12	16
var. Commeliniana		4	12	16
var. portoricensis		4	12	16
Zamia floridana		4	12	16

In several genera, chromosomes are found with apparently terminal spindle fiber attachment points. These are especially clear as the chromosomes begin to separate at late metaphase. There is so much variation in chromosome size in different cells of a single individual that it was seldom possible to establish any consistent difference in chromosome size in different genera. The chromosomes of *Cycas* seem to be relatively shorter than those of other genera. The relative lengths of the chromosomes and the positions of the spindle fiber attachment points are consistent within each genus.

The chromosome number and morphology may differ considerably in different genera but the genoms of the species within each genus seem to be very similar, a condition also found in the Coniferales (Sax and Sax 1933). *Zamia* and *Ceratozamia* are similar in chromosome number and morphology. According to Chamberlain (1926) these genera have been crossed and the *Zamia* (male) parent was found to be dominant in F_1. Both the cytological and genetic data would indicate that these two genera are closely related.

The chromosome numbers in the cycads differ from those in the typical conifers. The basic haploid numbers are 8, 9, 11, and 13 for the cycads and the lower numbers 8 and 9, are most characteristic. In the conifers the basic number is 12 for the Taxaceae, although recent studies indicate that *Podocarpus* has 20 pairs of chromosomes. The basic number is 12 for most *Abieteae* and 11 for the *Cupresseae* and *Taxodieae,* with the exception of *Sciadopitys* which has 10 pairs of chromosomes. The basic chromosome numbers are 12 for the Ginkgoales and 7 for the Gnetales. The chromosomes are large in most gymnosperms, but *Gnetum* has a large number of relatively small chromosomes.

In general the chromosome numbers show some correlation with the taxonomic grouping of the gymnosperms. There is, however, little cytological evidence for any relation between existing gymnosperms and the angiosperms. If the angiosperms have been derived from the gymnosperms we must go back to extinct forms for the ancestral types.

SUMMARY

The haploid chromosome numbers in the Cycadaceae are as follows: *Cycas* 11, *Bowenia* 9, *Macrozamia* 9, *Stangeria* 8, *Encephalartos* 8, *Dioon* 9, *Microcycas* 13, *Ceratozamia* 8, and *Zamia* 8. Different genera may vary considerably in chromosome morphology, but species within each genus have similar chromosomes.

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EXPLANATION OF PLATES

PLATE 107

Photographs of cycad chromosomes. Aceto-carmine smears of root tips.
Photo. 1. Cycas revoluta.
Photo. 2. Microcycas calocoma.
Photo. 3. Zamia media var. portoricensis.
Photo. 4. Zamia pumila.

PLATE 108

Chromosomes of cycads.
Aceto-carmine smears. × 1000.
Figs. 1-7 from root tip cells. Fig. 8 from endosperms.

Fig. 1. Cycas revoluta.
Fig. 2. Cycas "Wadel."
Fig. 3. Macrozamia tridentata.
Fig. 4. Stangeria paradoxa.
Fig. 5. Encephalartos Altensteinii.
Fig. 6. Dioon spinulosum.
Fig. 7. Ceratozamia mexicana.
Fig. 8. Zamia media var. Gutierrezii.

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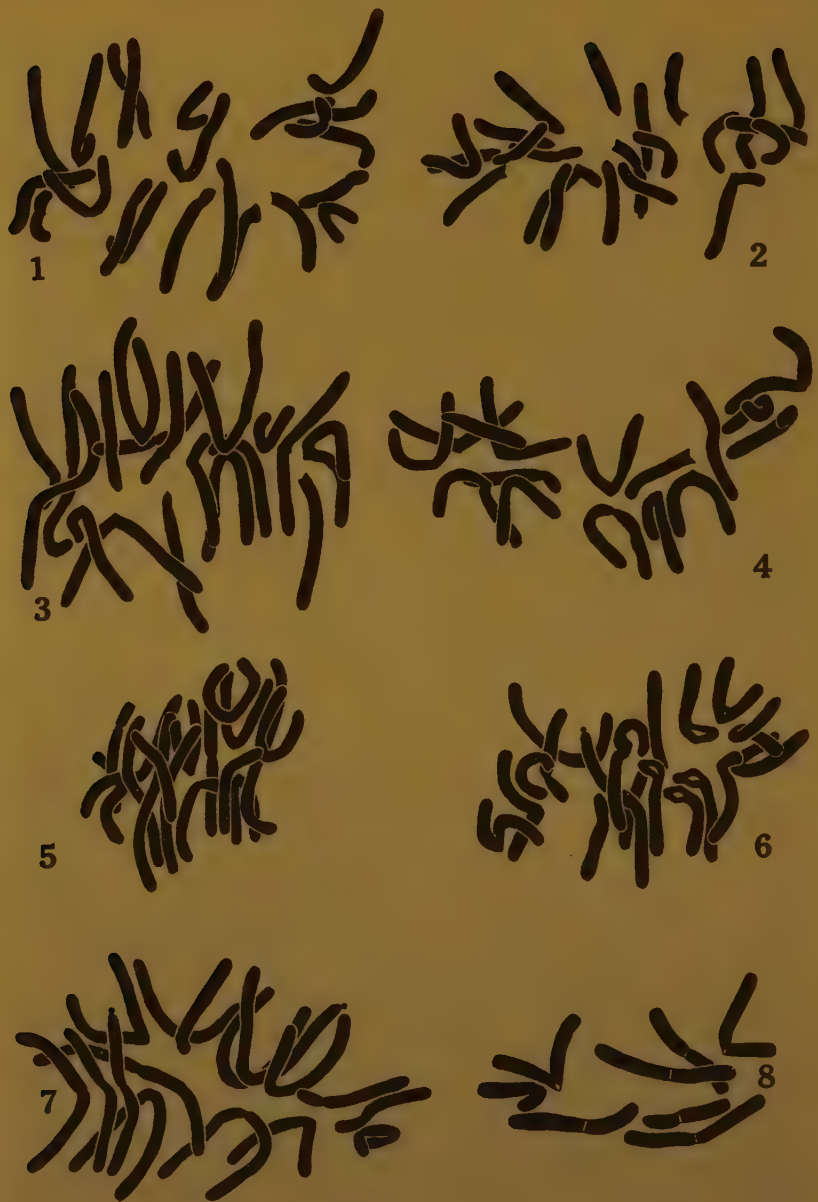
DEPARTMENT OF BOTANY, UNIVERSITY OF CHICAGO.

Chromosomes of the Cycadales

THE HELIOTYPE CORP. BOSTON



Chromosomes of the Cycadales

THE SEVENTH CENTURY OF THE RELIQUIAE FARLOWIANAE

DISTRIBUTED BY THE FARLOW HERBARIUM OF HARVARD UNIVERSITY

David H. Linder

With plate 109

The seventh century of the Reliquiae Farlowianae is being issued as a memorial to the late Professor Roland Thaxter and as a token of appreciation for the many valuable services that he rendered the Farlow Herbarium during his career as a mycologist. Since, during the latter days of his life, Professor Thaxter explicitly stated that it was his wish that the specimens be utilized for the continuation of the Reliquiae Farlowianae, and also that he did not wish another set to be issued under his name, the seventh century becomes a memorial not only to Professor Thaxter but also a tribute to his devotion and loyalty to his former teacher, Professor W. G. Farlow.

Because of the nature of the seventh century, it is composed almost exclusively of specimens collected by Professor Thaxter himself, and therefore it includes types of many of the species which he found opportunity to publish in the earlier days of his career. Since such is the case, many mycologists who have been under the impression that Professor Thaxter's interests were solely confined to the Laboulbeniales, may be surprised to learn how broad his interests really were. To those who were more intimately acquainted with him, and who must often have been impressed by his accurate and detailed knowledge of widely separated groups of fungi, it is hoped that this century of the Reliquiae Farlowianae may recall pleasant associations.

Many of the specimens of this set have been determined by specialists but a large number were named by Professor Thaxter himself, and since the names assigned by him represented his ideas, they have been retained. Undoubtedly, had time permitted, he would have changed many of the names to conform with the nomenclature of more recent monographic treatments. Accordingly, in a few instances the preferable name, as accepted in the Bibliographic Index of the Farlow Herbarium, has been added below that assigned by Professor Thaxter. The same remarks also apply to a few of the Uredinales which were determined by Professor J. C. Arthur. The lichens have been treated in a similar manner and the names accepted by Zahlbruckner have

been added in order that the nomenclature conform to that in the Catalogus Lichenum Universalis.[1]

As was true of the previous six centuries, this one will shortly be sent out to various botanical institutions in this country and abroad. Because of the fact that only thirty-six sets are available for distribution, preference will be given to those institutions which already possess the first six centuries, and especially to those which have sent specimens in exchange for the sets already issued. Should any institution that has already received the earlier centuries of the Reliquiae Farlowianae not receive this continuation within a reasonable length of time, the writer, upon notification, will be only too glad to rectify any oversight.

In connection with the issuing of this century, it is necessary to describe one new species, as represented by no. 629, namely *Phyllachora Buddleiae* Arnaud and an associated conidial phase. This specimen was sent to Professor Arnaud for determination and he returned it with the above name and a description, but stated that he did not intend to follow the matter further. Accordingly the description follows:

Phyllachora Buddleiae Arnaud, sp. nov. Plate 109

Fructificationes numerosae, minutae, atrae, orbiculatae et leniter rotundato-elevatae, 200-350 μ diam., maculis orbicularibus, discoloribus, 0.3-2 cm. diam. superne insidentes; clypeo atro amphigeno vel raro tantummodo epigeno, 72-285 μ diam., 10-72 μ crassitudine, clypeo supero ostiolato; loculis solitariis subglobosis vel applanatis, 243-360 × 126-255 μ, parietibus tenuibus, hyalinis vel subhyalinis; ascis late clavatis, 72-100 × 19.5-31 μ, octosporis; sporidiis irregulariter distichis, oblongis, utrinque obtusis, continuis levibus hyalinisque, 19.5-25.5 × (12.5)-14.5-16.5 μ; paraphysibus hyalinis, filiformibus, tenuibus, flexuosisque, simplicibus vel interdum parce ramosis, 72-90 × 2.5-3.5 μ.

Fructifications numerous, appearing as black rounded and somewhat elevated dots, 200-350 μ in diameter, formed on the upper surface of the leaf in the irregularly circular, discolored areas which are 0.3-2 cm. in diameter. The clypeus is black, amphigenous or occasionally only epigenous, irregularly developed and variable in size, 72-285 μ in diameter, 10-72 μ thick, the dorsal clypeus ostiolate. The locules, formed in the mesophyll of the leaf, are sub-

[1] Zahlbruckner, A. Catalogus Lichenum Universalis. vol. 1-9: 1922-33. Borntraeger, Leipzig.

globose to depressed globose, rarely more than one in a stroma, 243-360 μ in diameter, 126-255 μ high, with slender hyaline or subhyaline walls. The asci are broadly clavate, 72-100 × 19.5-31 μ, 8-spored. The ascospores are irregularly distichous, hyaline, smooth, broadly ellipsoid, both ends bluntly rounded, 19.5-25.5 × (12.5)-14.5-16.5 μ. Paraphyses hyaline, 72-90 × 2.5-3.5 μ, straight or flexuous, simple or occasionally branched below.

On *Buddleia Humboldtiana* Roem. & Schult., Valley of Mexico, Mexico, Oct. 3, 1895, *Pringle*.

Accompanying *Phyllachora Buddleiae* and within the same discolored area, the conidial stage is frequently found. To this the writer gives the name *Phleospora Buddleiae* in the belief that, wherever possible, the conidial stages should also be recorded in order that at some future date they may serve as definite characters for the natural arrangement of the ascigerous phase.

Phleospora Buddleiae Linder, sp. nov.

Acervulis (pycnidiis?) socio *Phyllachora Buddleiae* Arn., solitariis, paucis, epigenis, subepidermicis, 228-342 × 110-135 μ, pariete superne tantum e contextu mutatis matricis formato; hypostromate tenui, hyalino vel subhyalino; conidiophoris paliformibus parallelis, 7-8 × 1.8-3 μ simplicibus vel breve-ramosis, 1-3-septatis, cellula terminali in denticulum cylindricum rotundato-fastigata; conidiis 9-11 × 0.5-1 μ, hyalinis, cylindricis vel leniter fastigatis, 1-septatis, cellulis duabus ad septum facile separantibus.

Acervuli or pseudo-pycnidia in the dead areas in association with *Phyllochora Buddleiae* Arn., few, solitary, epigenous, subepidermal but later erumpent; the upper part of the pseudo-pycnidium is composed of discolored host cells which form the clypeus; the thin hypostroma is hyaline or subhyaline. The conidiophores are closely arranged in a palisade-like layer and are simple or short-branched, 7-8 × 1.8-3 μ, 1-3-septate, the terminal cell tapering to an elongate sporogenous tooth. The conidia are hyaline, cylindric or tapering, 9-11 × 0.5-1 μ, 1-septate, the cells readily breaking apart at the septum.

The specimen of *Gymnosporangium Ellisii* (Berk.) Farlow *I* (no. 675) is of interest in that it demonstrates that Professor Thaxter, to the very end of his career, maintained his interest in the genus of rusts to which this species belongs. The specimens issued under no. 675 are the results of inoculation experiments made by Professor Thaxter

at his summer home at Kittery Point, Maine, with teleutospores obtained by him from Portsmouth, New Hampshire.

A word should also be said in explanation of the inclusion of the common *Lycoperdon piriforme* Schaeff. Although the specimen was determined by the late C. G. Lloyd, Dr. Thaxter made a notation to the effect that it seemed to be *L. coloratum*. Which determination is correct, or whether *L. coloratum* is a valid species, the writer does not feel qualified to state. It is hoped, however, that by calling attention to this point, some student of the group will be enticed to solve the problem.

The task of sorting, preparing, and labeling the specimens of this century of the Reliquiae Farlowianae has been carried out by Mrs. L. W. Riddle, while the checking of names and authorities has been done by Dr. Grant D. Darker. To both of these members of the Farlow Herbarium staff, the Herbarium is greatly indebted.

PLATE 109

All drawings are made with the aid of the camera lucida at the approximate magnifications indicated below.

Fig. 1. Photograph to show a typical diseased area with the numerous more or less concentrically arranged fruiting bodies.
Fig. 2. Ascus to show partially distichous arrangement of the 8 broadly ellipsoid ascospores. × 1000.
Fig. 3. A single conidiophore with a slender elongation on which is borne a conidium. × 2230.
Fig. 4. Conidia showing the broad central septum at which the two cells break apart. Two of the conidia are unbroken. × 2230.
Fig. 5. A group of conidiophores from the closely packed palisade-like sporogenous layer. × 1000.
Fig. 6. Section through a fruiting body imbedded in leaf tissue, to show the upper and lower clypeus, the ostiole, the arrangement of the asci, and the numerous filiform paraphyses. × 130.
Fig. 7. Section through an "acervulus" to show the ruptured "clypeus" which consists for the most part of discolored epidermal tissue. × 130.

FARLOW HERBARIUM,
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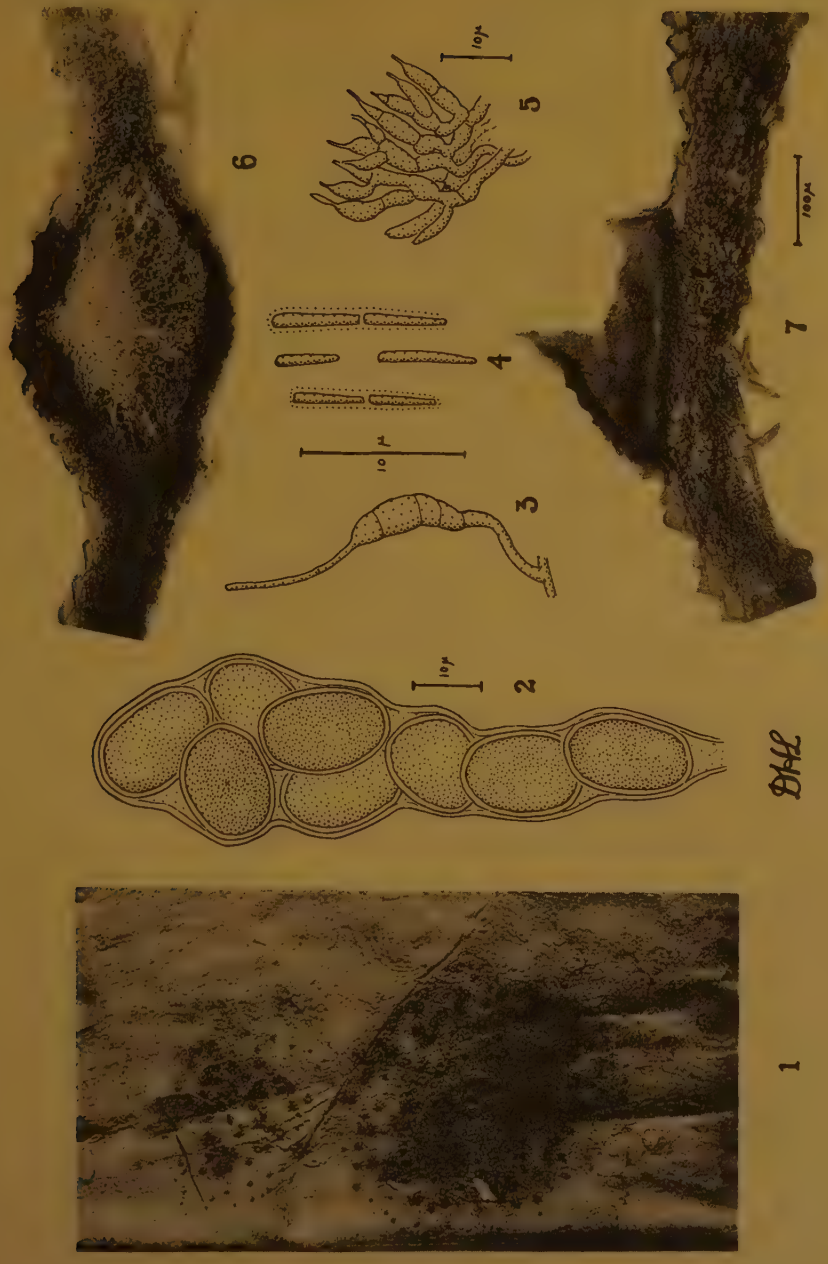

Phyllachora Buddleiae Arnaud

NOMENCLATURAL PRIORITY IN THE UREDINALES[1]

J. C. Arthur

In formulating the International Rules of Botanical Nomenclature,[2] which were the result of deliberations at the Botanical Congress of 1905 and 1910, the year 1753 was selected for the beginning of nomenclature for the various classes of plants, with a few exceptions, among them being that of the Uredinales (see Art. 19). The attempt to exclude from recognition in each group all names antedating the earliest important general treatise using binomial nomenclature led to the selection of Persoon's Synopsis Methodica Fungorum of 1801 as a starting point for the rusts and some other fungi.

As the Rules are formulated with the avowed purpose of promoting so far as possible uniform procedure in the use of botanical names it is pertinent to inquire if the exception for the starting point for the Uredinales was well selected and whether it meets that end. The question at issue is not one of theory, sentiment or individual preference, but one of facts which can be demonstrated by statistics. If the valid species of rusts established in the forty-eight years between 1753 and 1801 tend to disturb the uniform usage of subsequent years the exception to the general Rule is justified. On the contrary, if the exception introduces disturbance or uncertainty in subsequent usage, the exception should be cancelled. To understand the situation it is well to review the establishment of genera and species antedating Persoon's publication of 1801.

The only genera of the Uredinales proposed during that period were *Aecidium,* 1791, and *Uredo* and *Puccinia,* 1794, each erected by Persoon. As these genera were recognized in the Synopsis of 1801 which one of the alternate dates is accepted for their establishment is immaterial. Before these dates species of rusts had been referred to *Tremella, Lycoperdon* and *Ascophora,* all non-rust genera.

During this interval of forty-eight years between 1753 and 1801 a comparatively small number of rust species were described. If we exclude names applied to aecidial stages, as the International Rules require, and all duplicated names and synonyms, there are left to be

[1]Contribution from the Department of Botany, Purdue University Experiment Station.

[2]Briquet, John. Règles Internationales de la Nomenclature Botanique, 110 pp., June, 1912.

considered in this connection only twenty-six names by six authors, viz.: Linnaeus (1753), Dickson (1785), Jacquin (1788), Schrank (1789), Tode (1790) and Persoon (1791-99). The majority of these twenty-six names were accepted by Persoon in his Synopsis without change, except to transfer to the genus *Uredo* such as were formerly in *Lycoperdon* and *Aecidium*.

Out of this list of twenty-six names, published prior to 1801, only the following residue of eight names that were not transferred to the Synopsis without change would be affected by an earlier date for the beginning of priority, all being founded, irrespective of generic assignment, upon the "perfect state," and all but one (*Uredo Helioscopiae*) on the teleutosporic form.

Antedating 1801		Synopsis, 1801
Aecidium fuscum Pers.	changed to	Aecidium Anemones Pers.
Tremella Sabinae Dicks.	" "	Puccinia Juniperi Pers.
Ascophora disciflora α Tode	" " "	mucronata Pers.
Puccinia Polygoni Pers.	" " "	Polygoni-Aviculariae Pers.
Lycoperdon caryophyllinum Schr.	" "	Uredo Dianthi Pers.
Uredo Helioscopiae Pers.	" " "	Euphorbiae-Helioscopiae Pers.
Uredo Fabae Pers.	" " "	Viciae-Fabae Pers.
Uredo appendiculata β Pisi Pers.	" " "	appendiculata β Pisi-sativae Pers.

To justify the acceptance of 1801 for the beginning of rust nomenclature it must be shown that the eight names in the column for 1801 have been used by the majority of systematic uredinologists in preference to those antedating 1801. A search of the literature shows, however, that for more than a hundred years six out of the eight names were either not used at all, or only by one or two authors. *Uredo Dianthi* Pers. had been accepted by a few authors, while the one name receiving the greatest favor was that of *Puccinia mucronata* Pers., which was used by Strauss, 1810, Fries, 1815, Martius, 1817, Schlechtendahl, 1824, and some later authors, but since 1895 has been generally dropped in recognition of the earlier name. On the whole the usage up to the promulgation of the International Rules has been overwhelmingly in support of the names antedating 1801.

The usage of authors in general certainly shows no decided preference for the eight names of 1801 over the names previously established. For weightier evidence regarding the unbiased recognition of the earli-

est names that should be accepted it is best to turn to the more recent standard systematic works by authors of recognized ability, who had the facilities and inclination to make a careful taxonomic study. The following six standard works can be taken as a consensus of scholarly opinion regarding a suitable recognition of priority among the Uredinales.

Sydow (P. & H.), Monogr. Ured., 1902-15, use all the original eight specific names and none of 1801. The other five authors each employ all but one of the original eight specific names, and the exception is not taken from Persoon's Synopsis of 1801. They are:

Winter, Pilze Deutschl., 1881.
Fischer, Ed., Ured. der Schweiz, 1904.
Trotter, Flora Ital. Crypt., Ured., 1908-14.
Grove, British Rust Fungi, 1913.
Klebahn, Krypt.-Fl. Mark, Brandenburg, 1914.

No systematic work generally accepted as standard, which includes the eight names here considered, and which covers a wide geographical area, has been omitted from this list.

These facts undeniably show that the point of departure for nomenclature for the Uredinales in order to secure "fixity of names" and be "used by the great majority of naturalists in all countries," should be Linnaeus, Species Plantarum, 1753, and not Persoon, Synopsis Methodica Fungorum, 1801.

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NOTES

Trees of the Southeastern States. — From the University of North Carolina Press comes an attractive illustrated book of 399 pages on the Trees of the Southeastern States, by W. C. Coker and H. R. Totten.

The region covered, including the states of Virginia, North and South Carolina, Georgia and the northern part of Florida, is one of exceptional interest for students of trees. Some idea of the richness of its forest flora may be had from the fact, as stated in the preface to this book, that there are many more kinds of native trees in North Carolina alone than in the whole of Europe, and as examples of the large development of some of the tree genera it is interesting to note that there are 11 species of pine, 10 of hickory, 29 oaks, 9 magnolias and 13 lindens amongst the 227 native trees described.

The contents of the book include a brief introduction and key to the genera, followed by descriptions and keys to the different species, and in addition a great amount of interesting information on the local range, abundance, and economic value of the different trees, much of which is presented in an original way or is based upon the personal observations of the authors. There is also a short bibliography and glossary for the use of students.

While the treatment is scientific and follows the arrangement of other tree manuals, the language has been designedly made as simple as possible and technical terms are generally avoided or translated both in the keys and in the descriptions, so that they will be readily understood even by those who have very little botanical knowledge. The original outline drawings, showing the leaves, flowers, and fruits of the different trees add greatly to the value of the work. These are very well done, and they bring out clearly the distinctive characters of the different species.

Although designed primarily for students of botany and of forest trees in the southeastern states, and naturally of the greatest value to them, this little book cannot fail to be of interest to tree students everywhere. — ERNEST J. PALMER.